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Lakeward Migrations by Juvenile Atlantic Salmon, *Salmo salar*

Jeffrey A. Hutchings

Department of Biology, Memorial University of Newfoundland, St. John's, Nfld. A1B 3X9

Hutchings, J. A. 1986. Lakeward migrations by juvenile Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. 43: 732–741.

Atlantic salmon parr, *Salmo salar*, undertook lakeward migrations from outlet streams in the Wings Brook system, eastern Newfoundland. Lakeward movement occurred from May through November, intensifying over a 6- to 8-wk period during spring. Parr remained in the lakes where they either matured (usually males) or smoltified (predominantly females) before returning to the streams. Mature parr emigrated from the lakes during autumn whereas smolts entered the streams during spring. Lakes provided conditions for increased parr growth and survival to the smolt stage relative to the riverine environment, and appeared to represent important overwintering habitat. Smolt production occurred almost entirely within the lakes. Parr movement into lakes could not be explained by physical environmental factors. Lakeward migrations appear to have an adaptive basis and can be explained as an evolutionarily stable reproductive tactic.

Le tacon de saumon atlantique, *Salmo salar*, a entrepris sa migration vers les lacs depuis les émissaires du bassin du ruisseau Wing, à l'est de Terre-Neuve. Le mouvement vers les lacs a eu lieu de mai à novembre et s'est intensifié pendant 6 à 8 sem au printemps. Le tacon reste dans les lacs jusqu'à ce qu'il devienne mature (habituellement les mâles) ou smolt (surtout les femelles) avant de retourner dans les cours d'eau. Le tacon mature a quitté les lacs en automne et le smolt est entré dans les cours d'eau au printemps. Les lacs offrent des conditions favorables à la croissance du tacon et à sa survivance jusqu'au stade smolt qui a lieu en milieu riverain, et semblent être des lieux d'hivernage importants. La production du smolt s'est faite presque entièrement dans les lacs. L'entrée du tacon dans les lacs n'a pu être expliquée par des facteurs environnementaux physiques. Les migrations vers les lacs semblent être un moyen de s'adapter et peuvent être interprétées comme une tactique de reproduction stable sur le plan de l'évolution.

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Migration is thought to be an adaptive phenomenon that enhances reproductive fitness through increased growth and survival (Heape 1931; Nikol'skii 1963; Harden Jones 1968; Northcote 1978, 1984). Migrations undertaken during juvenile stages affect fitness if the habitats involved are sufficiently heterogeneous to impart differential growth and survival. These migrations can have considerable influence on production because both mortality rates and numbers of individuals are highest during early life history (Northcote 1978). This is an important consideration from both a management and an ecological perspective. Successful management is contingent upon thorough knowledge of the habitats used by a species throughout its life. For migrating salmonids, it is necessary to identify the mechanisms responsible for initiating various movement patterns, and to assess the importance of these movements to a species' production. From an ecological perspective, varying patterns of migration can strongly influence life history strategies (Hutchings and Morris 1985). A study of movement patterns can, then, lead to an understanding of how these strategies may arise and persist through time.

Many salmonids migrate between lacustrine and riverine environments. These migrations can result in enhanced growth, increased reproductive success, or avoidance of unfavourable environmental conditions (Northcote 1978; Godin 1982). The usual pattern is for all juveniles within a cohort to move into a lake within the first 2 yr of life, feed and grow in the lake, and then return to their natal streams either to spawn or to migrate to sea (Godin 1982).

Atlantic salmon parr, *Salmo salar*, of anadromous parents are known to occur in ponds and lakes (Pepper 1976; Chadwick and Green 1985) yet little is known of the lakeward movements by juveniles. Stuart (1957) noted that salmon parr accompanied juvenile brown trout, *S. trutta*, in a spring upstream migration from a Scottish reservoir into an inlet stream, and then returned to the reservoir in autumn. Pepper (1976) found a similarity in scale characteristics between smolts captured at the outlet of Salmon Pond, Newfoundland, and parr in the lake and in an inlet stream. He concluded that parr moved from the inlet into the lake between the ages of 1 and 4 yr. Salmon parr have been reported to move into small inlet streams from Vangsvatnet Lake, Norway, during the spring and return to the lake to overwinter (B. Jonsson, pers. comm., cited in Northcote 1984).

The objectives of this paper are to describe lakeward migrations by juvenile Atlantic salmon and to assess the importance of lacustrine habitat to salmon production. Migration is defined here as directed (i.e. nonrandom) movements occurring with regular periodicity that result in an alternation between two or more separate habitats (cf. Northcote 1984).

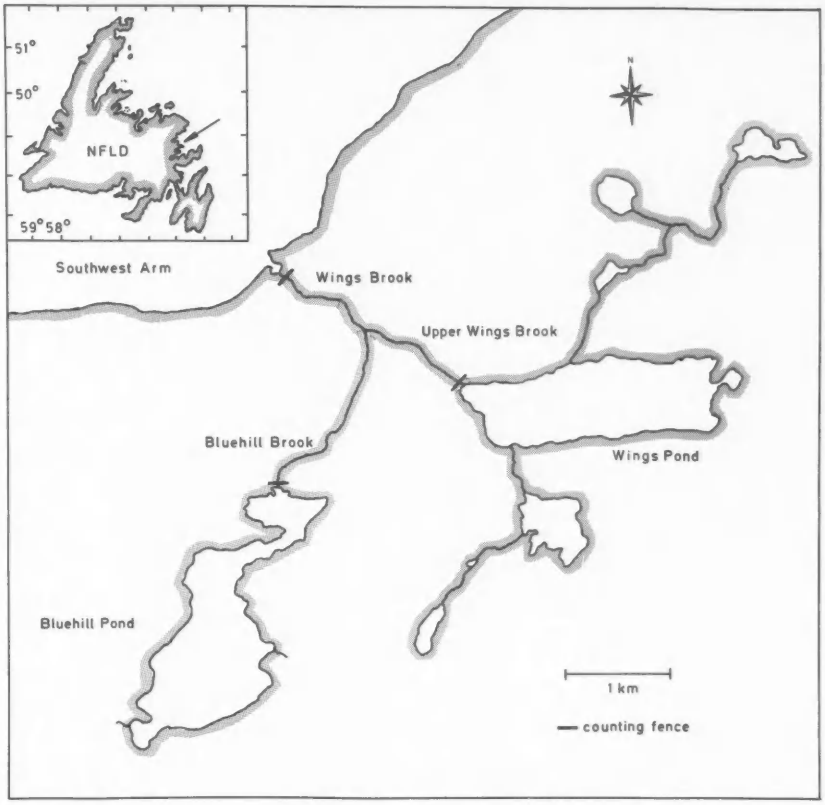

FIG. 1. Wings Brook system, Bonavista Bay, Newfoundland.

Study Area

Wings Brook and its associated lakes, Wings Pond and Bluehill Pond, are located within Terra Nova National Park in eastern Newfoundland (Fig. 1). The winters are moderately cold and the summers warm (e.g. mean maximum 1983 January and July air temperatures were −1.0 and 22.9°C, respectively). The lakes are generally ice free from mid-April to late December.

The lake outlets, Upper Wings Brook and Bluehill Brook, are second-order streams that converge to form the main stem of Wings Brook 1.03 km from its mouth. The brook flows into a small (0.8 ha), shallow (z_{mean} = 0.6 m), soft-bottom basin before emptying into a deep (z_{max} > 34.0 m) and expansive (length = 6.0 km, $width_{max}$ = 0.5 km) estuary, the southwestern arm of Alexander Bay (Bonavista Bay).

The fluvial environment of the Wings Brook system is small (total area = 1.4 ha; maximum 1982–83 discharge = 1.1 $m^3 \cdot s^{-1}$) in comparison with most rivers supporting Atlantic salmon (see Porter et al. 1974). Short stretches of rapids exist but vertical heights do not exceed 40 cm. Shallow riffle (83%) and run (12%) sections are abundant whereas deep pool habitat is scarce (terminology follows Rimmer et al. 1983). Bottom substrate is predominantly cobble/pebble (16–256 mm in diameter) although a 20-m section of Bluehill Brook is composed wholly of sand (0.06–2.00 mm in diameter).

Bluehill Pond is a large (128 ha) lake with two distinct basins connected by a shallow channel. The north basin is much smaller (16.4 ha; z_{mean} = 2.65 m; z_{max} = 10.5 m) than the south basin (111.4 ha; z_{mean} = 9.23 m; z_{max} = 22.6 m). Small, intermittant streams empty into the lake. The lake supports populations of anadromous and nonanadromous Atlantic salmon and brook trout, *Salvelinus fontinalis*, nonanadromous Arctic char, *S. alpinus*, rainbow smelt, *Osmerus mordax*, and American eel, *Anguilla rostrata*.

Wings Pond (121.2 ha; z_{mean} = 7.2 m; z_{max} = 19.5 m) is a single-basin, rectangular lake that deepens gradually around its periphery. Unlike Bluehill Pond (south basin), Wings Pond does not thermally stratify (Kerekes 1974; Hutchings 1985). The lake supports populations of anadromous and nonanadromous Atlantic salmon and brook trout, rainbow smelt, American eel, threespine stickleback, *Gasterosteus aculeatus*, and fourspine stickleback, *Apeltes quadracus*. Inlet populations are restricted to brook trout in a southern stream.

There is strong evidence that anadromous and nonanadromous *S. salar* represent within-population variation in the Wings Brook system. This is supported by the low probability of spatial reproductive isolation between forms in the outlet streams (Hutchings 1985), an absence of behavioural isolating mechanisms preventing interbreeding (Hutchings and Myers 1985), and the equivalency of mitochondrial DNA sequences between forms in the Wings Brook system (U. Gyllensten, Department of Genetics, University of Stockholm, Sweden, pers. comm.).

TABLE 1. Dates of counting fence operations.

Station	Trap section	Dates of operation
Wings Pond	Upstream	June 9 – November 23, 1982
		May 5 – September 28, 1983
	Downstream	May 21 – November 23, 1982
		May 5 – September 28, 1983
Bluehill Pond	Upstream	June 1 – November 22, 1982
		May 5 – September 28, 1983
	Downstream	May 28 – November 22, 1982
		May 5 – September 28, 1983

Materials and Methods

Fish Collections

Two-way counting fences (Anderson and McDonald 1978) were maintained at the outlets of each lake and of the whole system to monitor upstream and downstream fish movements (Fig. 1). Traps were checked once or twice daily from May through November 1982 and May to October 1983 (Table 1). The fence materials used at the lake outlets (6-mm^2 square mesh screening) and at the estuary (steel conduit lined with black polyethylene) were such that all traps should have been 100% efficient in capturing parr greater than 40 mm in fork length (corresponding to a salmonine body depth of 8 mm (Scott and Crossman 1973)).

Salmon parr were counted, measured (fork length to the nearest 1 mm), and weighed (to the nearest 0.1 g) under anaesthetic of Alka-Seltzer® and water (i.e. by CO_2 saturation). All fish were released in their original direction of travel following recovery. Sexually mature males were identified by emission of sperm, and mature females by swollen tissue around the anus and presence of eggs at the urogenital opening. Scale samples were removed from the left side between the base of the dorsal fin and the lateral line, mounted on acetate slides in the field, and stored in labelled envelopes. Scales were aged under 40× magnification using a Bausch and Lomb microprojector, following criteria established by Havey (1959). Lengths at earlier ages were back-calculated using Lee's (1920) formula. Salmon parr were marked with a combination of partial pelvic and adipose fin clips (specific to trap location and direction of travel) to determine the period of residency in the lakes and streams following initial movement into these environments.

The trap at Wings Pond was checked twice daily on 53 occasions between May 15 and September 1, 1983, as a subelement of the general sampling program, to assess the diel timing of parr movements into the lakes and streams. Initial trap checks were conducted between 07:00 and 10:00, followed by a second census 1–4 h later.

Salmon smolts were removed from the traps by dip net and counted during the 1982 field season. In 1983, smolts emigrating from the lakes were marked with either a left (Wings Pond) or right (Bluehill Pond) half-pelvic fin clip. The proportion of migrating smolts leaving the system that originated in the lakes was determined by calculating the proportional yield of marked smolts emigrating from the stream into the estuary relative to the total number of smolts entering the estuary. Smolts were measured, weighed, and aged following the procedures outlined for parr. Gonads were removed from the first 118 smolts to pass through the estuary trap in 1983 and examined macroscopically for evidence of prior maturation.

TABLE 2. Total numbers of *Salmo salar* moving through the lake outlet counting fences.

Station	Parr	Smolts
1982		
Wings Pond		
Upstream	259	5
Downstream	840	322
Bluehill Pond		
Upstream	119	1
Downstream	368	30
1983		
Wings Pond		
Upstream	319	8
Downstream	32	462
Bluehill Pond		
Upstream	188	1
Downstream	70	187

Statistical Analyses

Relationships between physical environmental attributes known to influence salmonid migrations (see Northcote 1984) and daily movements of parr into lakes were examined using a stepwise multiple regression analysis. Environmental variables included maximum and minimum daily water temperatures (maxtemp, mintemp), daily average water level (depth), daily amount of precipitation (precip), and the difference between daily maximum and minimum water temperatures (tempdif), which is an approximation of the daily rate of temperature increase. To minimize bias in the analyses, time periods were restricted to the months of peak lakeward movement (May, June, July).

An analysis of covariance was employed to test for slope/intercept homogeneity between the linear relationships of scale radius with age for riverine and lacustrine parr. Growth rates of smolts from Wings and Bluehill ponds were compared in a similar fashion.

Differences in the mean scale radius attained by migrant (emigrating from the streams into the lakes), riverine, and mature parr at the end of their first winter were examined using an analysis of variance. Data were $\log_{10}$-transformed to satisfy the assumption of variance homogeneity among samples.

Results

Emigration from Streams into Lakes

Lakeward movements by salmon parr occurred from early May through late November at varying levels of intensity (Fig. 2; Table 2). The magnitude of these movements was greatest during a 6- to 8-wk period from mid-May to mid-July and a 2- to 3-wk period in autumn. In 1982, 64.8 and 25.0% of the total parr movement into Wings Pond occurred during these spring (from commencement of trap operations to July 14) and autumn (October 1 – November 22) periods, respectively. Spring and autumn figures for Bluehill Pond were 84.5 and 5.4%. The 1983 spring period accounted for 91.7 and 93.6% of the parr movements (May–October) into Wings Pond and Bluehill Pond.

Parr undertaking spring lakeward movements were predominantly 1 and 2 yr old (Fig. 3). Six underyearlings were captured in the upstream trap at Wings Pond (none were captured at Bluehill Pond) from May 1982 to September 1983. The

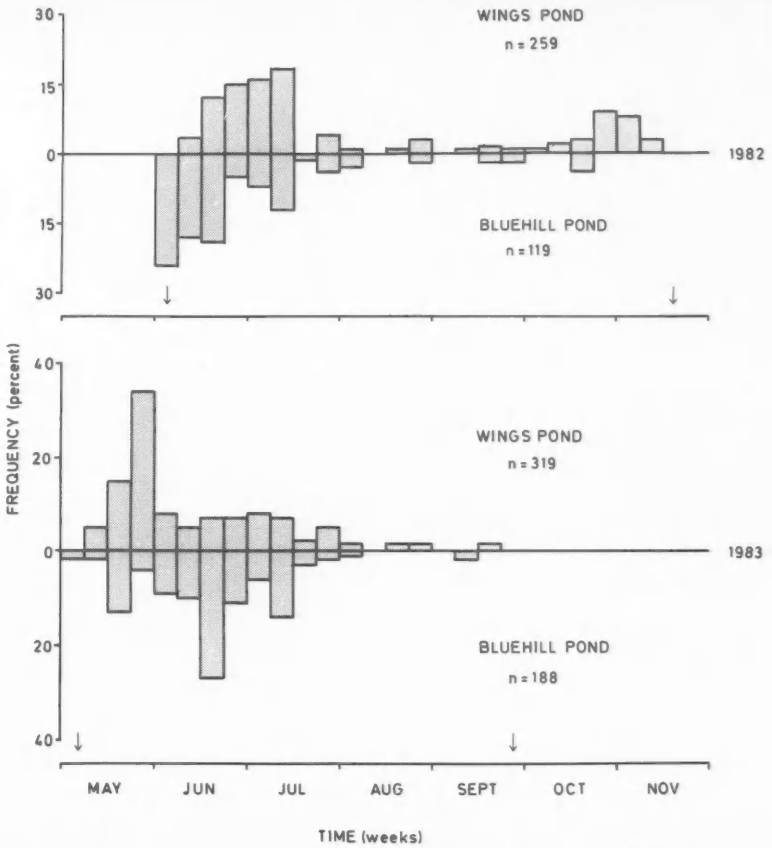

FIG. 2. Chronology of lakeward movements by salmon parr into Wings and Bluehill ponds from outlet streams. Each histogram represents the proportion of movements that occurred at each site, on a weekly basis, during the periods indicated. Arrows indicate dates of trap installation and removal.

shapes of the age–frequency distributions were very similar between lake sites within each year. Length–frequency distributions and corresponding mean values were also similar between and within sampling sites (Fig. 4).

In 1982, 2.6 and 20.0% of the total number of parr moving into Wings and Bluehill ponds, respectively, reentered the outlet streams prior to autumn. None of the parr moving into the lakes in 1983 had reentered the streams by autumn.

Lakeward movements were predominantly diurnal. The majority (51%) of parr entering the lakes were enumerated during the second census. Given the 7–11 h of daylight following the second census, this percentage is a minimum value.

Environmental parameters accounted for only a small proportion (8.1%; $p > 0.05$) of the variance in daily parr movements into Bluehill Pond in both 1982 and 1983 (Table 3; significant r^2 values effected by outliers). Orders of variable addition into the regression equation were as follows: 1982 — tempdif, minwater, depth, precip; 1983 — minwater, depth, tempdif, precip. Depth and tempdif explained 27.8% ($p < 0.0001$) and 7.5% ($p < 0.05$) of the variance in daily parr movements into Wings Pond during 1982 and 1983, respectively. Tempdif had the higher partial correlation with the criterion variable in 1982 whereas depth explained the greater variation in 1983.

TABLE 3. Variation in daily parr movements into lakes explained by five environmental factors (*significant at $p = 0.05$ level).

	Wings Pond		Bluehill Pond	
Parameter	1982 (r^2)	1983 (r^2)	1982 (r^2)	1983 (r^2)
maxwater	0.009	0.017	0.001	0.093*
minwater	0.005	0.000	0.040	0.157*
depth	0.121*	0.008	0.017	0.033
precip	0.004	0.011	0.030	0.028
tempdif	0.131*	0.071	0.076*	0.006

Sexually mature males comprised 92.2% of the 64 parr moving into Wings Pond during autumn in 1982. The sex of the remaining 7.8% was unknown. Males were in a spending or spent condition (sensu Jones 1959). Twenty-six spent males returned to Wings Pond the following spring.

Immigration into Streams from Lakes

Parr movement into outlet streams was infrequent during the spring and summer months, and involved few individuals (Fig. 5, 6). Peak spring and summer periods of lake emigration

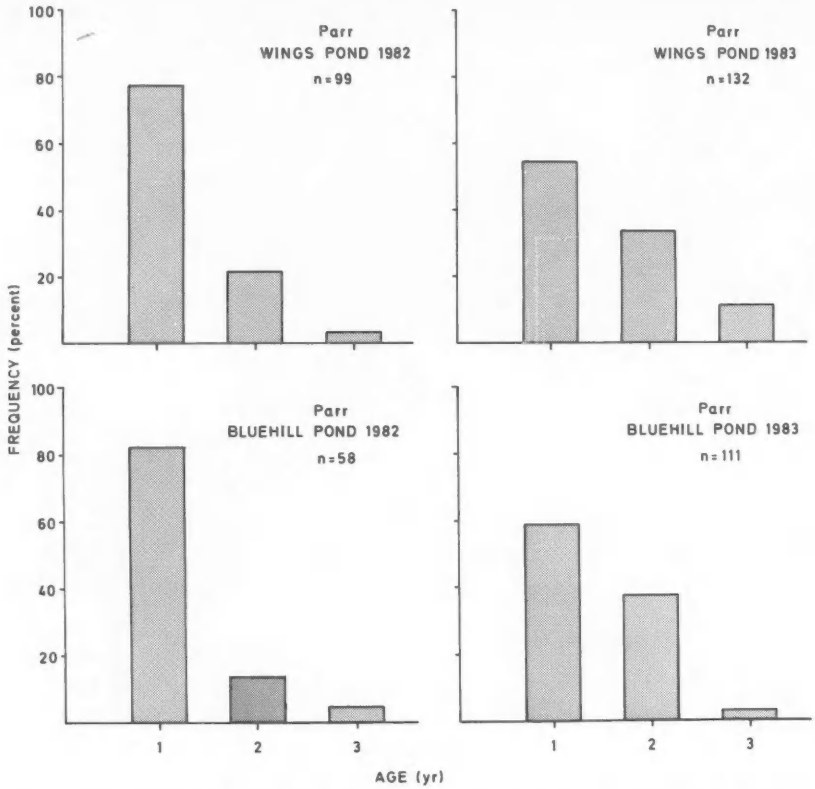

FIG. 3. Age–frequency distributions of salmon parr moving into Wings and Bluehill ponds from outlet streams prior to autumn.

were not evident, as the relative intensity of these movements was uniformly low. Downstream movements were predominantly nocturnal, as most parr (95%) were enumerated at the first census. These fish ranged from 1 to 3 yr in age, and their length frequency distributions lacked an obvious mode (Fig. 6).

The apparent randomness associated with the intermittent prespawning emigrations contrasted sharply with the timing and magnitude of the autumnal movement of parr into the streams. Parr emigration from both lakes increased substantially during the second week of October, reaching peak magnitudes by the end of the month before tapering off during mid-November (Fig. 5). Parr emigrating from Wings Pond included 764 sexually mature males (mean length 134 mm (70–247 mm)) and 10 mature females (mean length 358 mm (153–523 mm)). The spawning migration from Bluehill Pond included 301 mature males (mean length 139 mm (76–227 mm)) and 10 mature females (mean length 254 mm (220–312 mm)). Fin-clipping data indicated that at least 6 (120–166 mm) of 480 sexually mature males from Wings Pond migrated as smolts the following spring.

Smolts entered the outlet streams during May and June. The number of smolts emigrating from the lakes in 1982 (n = 352) exceeded the number eventually entering the estuary (n = 334). Fin-clipping studies indicated that 86.7% of the total number of smolts entering the estuary in 1983 (n = 633) originated in the lakes. Smolts leaving Bluehill Pond were significantly (Student's t-test; $p < 0.05$) older (mean = 4.8 yr) than those leaving Wings Pond (mean = 4.0 yr) (Fig. 7). Bluehill Pond smolts were also significantly ($p < 0.05$) larger (mean = 202 mm) than Wings Pond smolts (mean = 164 mm) (Fig. 8). The pooled sex ratio of smolts emigrating from the lakes was skewed in favour of females by 6.4:1.0. Gonadal examinations indicated that 37.6% (n = 6) of the male smolts, and none of the female smolts, had matured as parr.

TABLE 4. Summary of the scale radius (y) – age (x) regressions for parr and smolts in the Wings Brook system; equations are of the form $y = mx + b$.

Classification	Slope (m)	Intercept (b)	r^2	n
Lacustrine parr	11.41	−0.57	0.63	421
Riverine parr	7.73	−2.95	0.58	286
Wings Pond smolts	5.13	23.19	0.21	157
Bluehill Pond smolts	5.54	31.19	0.27	103

Growth

Lacustrine parr grew at a significantly ($p < 0.01$) faster rate than riverine parr (Table 4). Mean scale radius at the end of the first winter differed significantly (F_s = 25.12; $p < 0.01$) among mature, migrant, and riverine parr. Paired comparisons using least-significant differences between means indicated that mature male parr grew significantly ($p < 0.05$) faster in

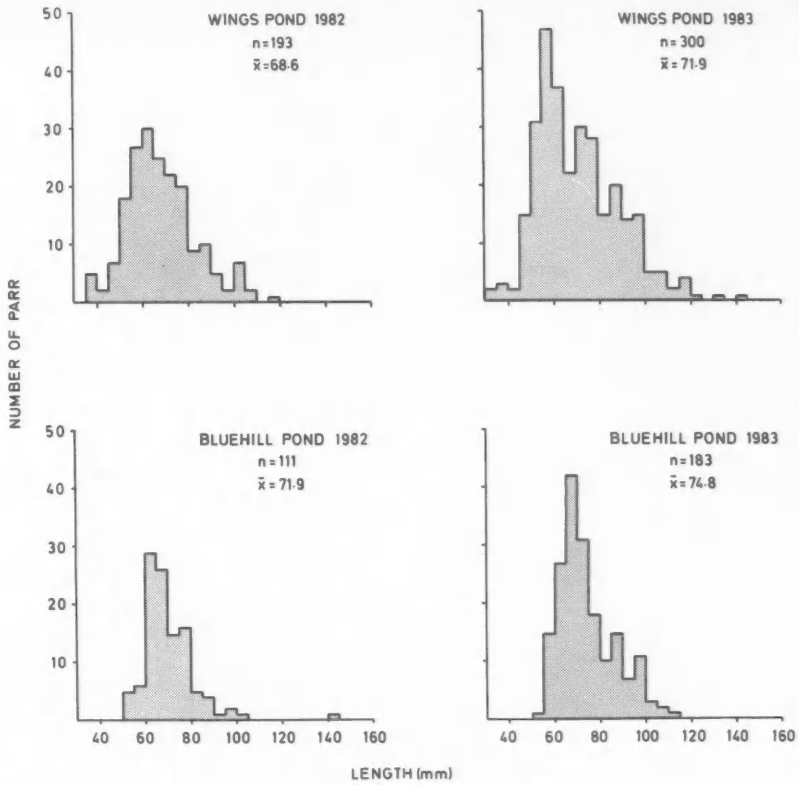

FIG. 4. Length–frequency distributions of salmon parr moving into Wings and Bluehill ponds from outlet streams prior to autumn.

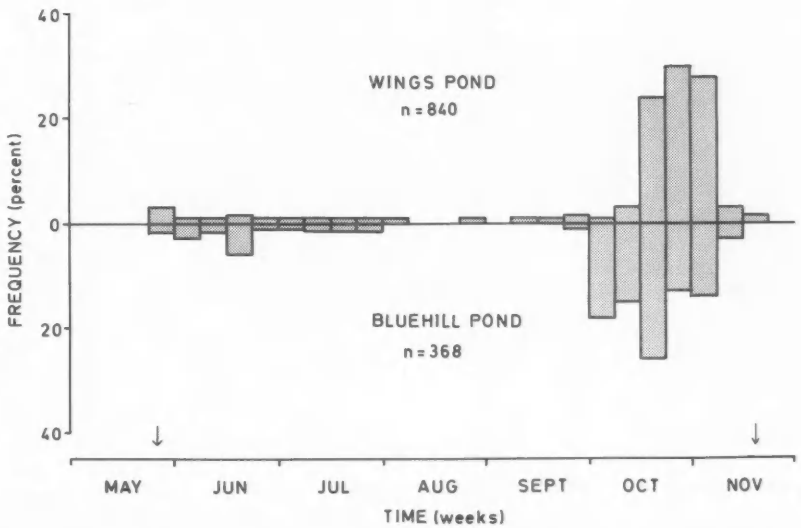

FIG. 5. Chronology of salmon parr movements out of Wings and Bluehill ponds in 1982. Each histogram represents the proportion of movements that occurred at each site, on a weekly basis, during the periods indicated. Arrows indicate dates of trap installation and removal.

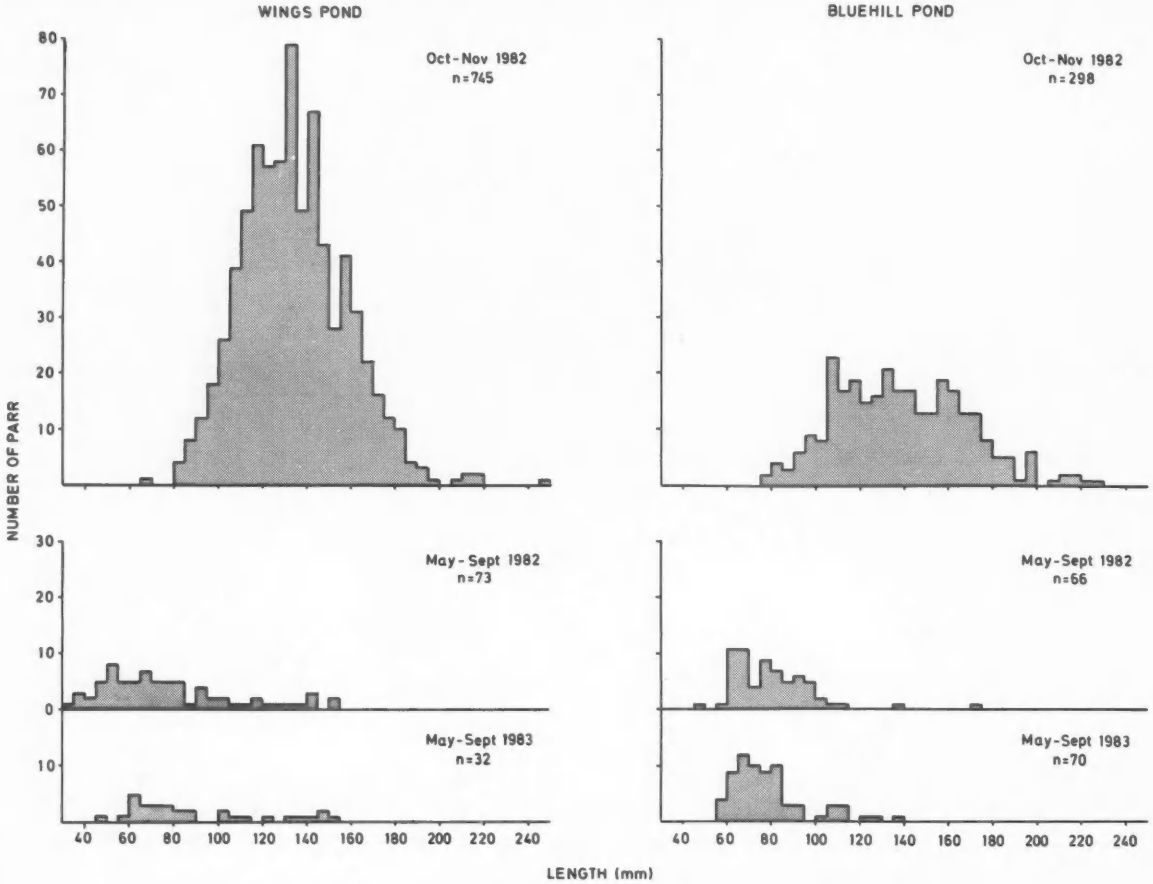

FIG. 6. Length–frequency distributions of salmon moving out of Wings and Bluehill ponds.

their first year of life than either migrant or riverine parr. Migrant and riverine parr did not differ significantly in growth during their first year. Growth rates of smolts (Table 4) were not significantly different ($p > 0.05$) between Wings and Bluehill ponds.

Discussion

Lakeward migrations by juvenile Atlantic salmon in the Wings Brook system can be summarized as follows. Anadromous and nonanadromous *S. salar* spawn in lake outlet streams during late October – early November (Hutchings 1985). The young emerge from the gravel in mid-June, and remain in the streams for at least 1 yr following which some undertake upstream, lakeward movements. These predominantly diurnal movements occur over a 6- to 8-wk period in the spring and are normally initiated by individuals in their second and third years of stream residence. Parr remain in the lakes until smoltification (mainly females) or maturation (usually males), whereupon they return to the outlet streams. Smolts (aged 2–7 yr) emigrate from the lakes during the spring and, following a 14- to 16-mo period at sea (Hutchings 1985), return to the stream as mature adults. Mature nonanadromous *S. salar* enter the lake outlets in the autumn (October–November). Minimum age at first maturity ranges from 1 (males) to 3 (females) yr. Spent parr may smoltify the following spring, or reenter the lakes either immediately after spawning or during the ensuing spring.

Lakeward migrations during juvenile life history stages are common among salmonids, notably rainbow trout, *Salmo gairdneri* (Northcote 1962, 1969), cutthroat trout, *S. clarki* (Raleigh 1971), brown trout (Thorpe 1974), brook trout (O'Connor and Power 1973), and sockeye salmon, *Oncorhynchus nerka* (McCart 1967). Migrations from outlet streams are predominantly diurnal, occurring among individuals ranging in age from 1–2 mo (sockeye salmon; McCart 1967) to 3–4 yr (brown trout; Runnström 1957). Water temperature and photoperiod are the primary physical environmental factors responsible for regulating these movements (Northcote 1969) although the initiation of lakeward migrations is largely controlled by innate rheotactic responses (Brannon 1967; Raleigh 1967, 1971; Raleigh and Chapman 1971; Bowler 1975; Kelso et al. 1981).

Arguments used to explain freshwater migrations by other juvenile salmonids have limited applicability to Atlantic salmon parr. Unlike the salmonids previously described, lakeward migrations by juvenile *S. salar* in the Wings Brook system are not undertaken by all members of the population

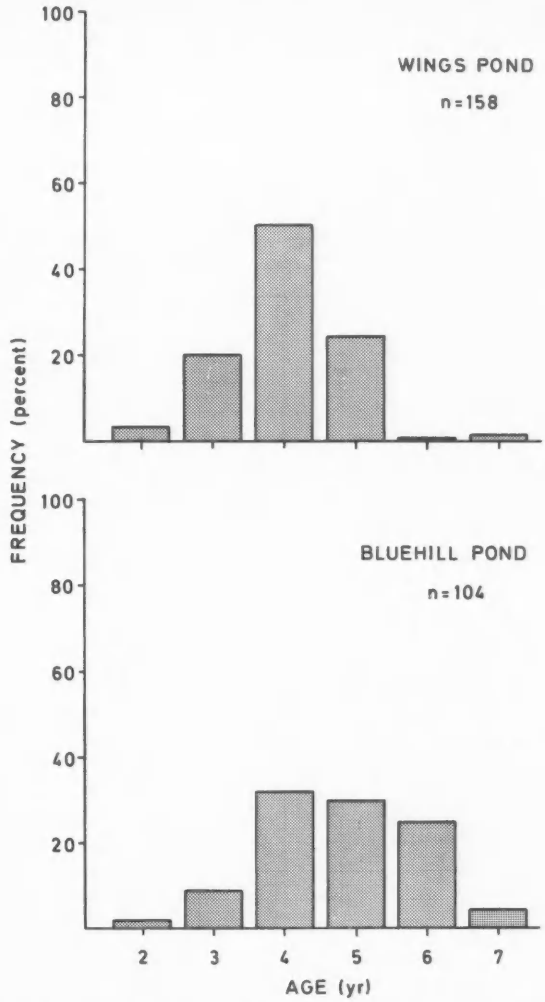

FIG. 7. Age–frequency distributions of salmon smolts emigrating from Wings and Bluehill ponds.

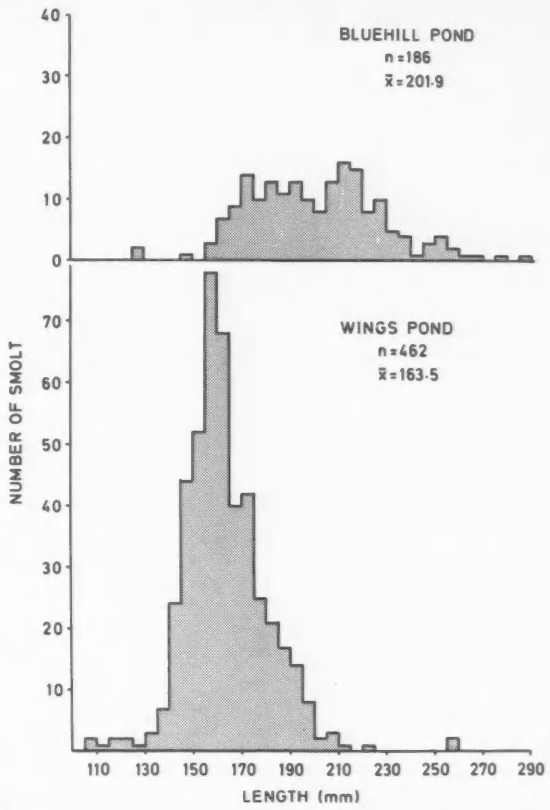

FIG. 8. Length–frequency distributions of salmon smolts emigrating from Wings and Bluehill ponds.

(Hutchings 1985). Therefore, any hypothesis used to explain lakeward migrations must account for the differential responses of parr to the factor(s) inducing this movement. This would weaken arguments based upon the contention that parr migrate simply to avoid unfavourable physical environmental conditions (e.g. high water temperatures, low water levels) because such influences would presumably have an equivalent effect on all individuals. Physical environmental factors generally accounted for less than 10% of the variation in lakeward movements by parr in the Wings Brook system. The relatively high amount of explained variation in lakeward movements at Wings Pond in 1982 (27.8%) does suggest, however, that water depth and rate of temperature increase can act in concert to regulate these movements once they have been initiated.

Lakeward migrations from outlet streams could result from intraspecific competition for limited stream habitat suitable for the establishment of feeding territories. This hypothesis is untenable for several reasons. First, subordinate individuals are normally displaced downstream by dominant fish (Chapman 1962; Gibson 1981; McNicol and Noakes 1981). Juvenile Atlantic salmon feed primarily on stream invertebrate drift (Wańkowski and Thorpe 1979), so upstream sections of outlet streams should be the preferred sites for feeding territories because drift invertebrate biomass increases with proximity to lake outlets (Gibson and Galbraith 1975). Second, competitive displacement of subordinate parr should be greatest when food supply is limiting (Symons 1971), yet lakeward movements occur when food resources are at their greatest abundance (Gibson and Galbraith 1975). Furthermore, since dominance is size related (Kalleberg 1958; Symons 1968), one would expect lakeward migrants to be the smaller individuals within and/or between age classes. However, growth of migrant parr did not differ significantly from that of riverine parr in the first year of life — the age at which most parr migrate. Finally, parr must negotiate a short series of rapids and relatively high vertical falls (5–10 cm) before entering Bluehill Pond. Such behaviour indicates a nonrandom movement rather than random displacement.

The low incidence of recaptured migrant parr at the lake outlets in 1982, and the absence of such recaptures in 1983, provide strong evidence that lakeward migrations were directed and nonrandom. Recaptures occurred during the first month of trap operations and could probably be attributed to the practice of returning parr into stream sections of moderate water velocity immediately above the entrance to the downstream trap. All recaptures were made within 3 d of clipping (81.5% within a

single day), suggesting that parr were carried into the downstream trap by the current, possibly as a result of fatigue or disorientation. Parr were subsequently released into still water either further upstream of the traps or directly into the lakes at the lake/stream confluence.

The suitability of lakes as juvenile salmon habitat is exemplified by the increased growth rates experienced by lacustrine parr relative to riverine parr. Abundant food resources, reduced energy requirements for maintaining position, and reduced competitive interactions among parr are probably the main factors contributing to this enhanced growth. Pepper (1976) reported growth rates among parr inhabiting a lake in central Newfoundland to be superior to those of parr in an inlet stream. Growth rates of salmon parr stocked into lakes in Quebec (Rimmer and Power 1978) and in the British Isles (Harris 1973; Pedley and Jones 1978) exceeded those of their riverine counterparts.

The relative yield of smolts in the riverine and lacustrine environments emphasizes the importance of lakes as overwintering habitat. The majority of smolts leaving the system originate in the lakes, yet the proportion of the population initially entering the lakes as parr is small (approximately 10% (Hutchings 1985)). This indicates that parr survival to the smolt stage is much higher in the lakes than it is in the streams. This may be due to a lack of suitable riverine overwintering habitat for large parr and presmolts. Deep pools comprise only a small proportion (13.5%) of the total stream area of Wings Brook. While it has been demonstrated that juvenile salmon will overwinter in sheltered chambers within the stream substrate (Smirnov et al. 1976; Gibson 1978; Rimmer et al. 1983), it has not been established that large parr or presmolts behave similarly. Increases in mortality rates with size have been reported for parr in riverine environments (Elson 1962; Myers 1984). This may account for the autumnal emigrations of large parr and presmolts in many rivers (Calderwood 1906; Saunders 1960; Meister 1962; Riddell and Leggett 1981; Youngson et al. 1983).

The adaptive significance of lakeward migrations is exemplified by the increased growth and survival experienced by lacustrine parr relative to riverine parr. A lakeward migration would, then, represent a suitable tactic to enhance individual fitness. Since only a portion of the population migrates into lakes, alternative tactics may exist for the remainder of the population. Some parr emigrate from the stream into the estuary, experience growth rates equivalent to those of lacustrine parr, and return to the stream following maturation (Hutchings 1985). In this context, parr migrations into lacustrine and estuarine habitat represent alternative reproductive tactics.

The argument can be further developed as follows. Given that size can be positively correlated with fitness (increased fecundity, increased survival, superior competitive advantage during spawning), a proportion of the parr population could be expected to adopt behaviours that would enhance growth and survival. The riverine environment is poor in terms of growth and survival for large individuals. Both the estuary and lakes provide conditions for increased growth although survival to maturity for estuarine parr is inferior to that of lacustrine parr (Hutchings 1985). If parr must emigrate from the stream to reduce size-specific mortality and increase growth (both of which should enhance fitness), then movements into the lakes and estuary could represent alternative reproductive tactics of which the latter is subordinate. Subordinate reproductive tactics can evolve to provide individuals with the opportunity to make the "Best of a Bad Situation" (BBS: Gross 1984) and be evolutionarily stable (Maynard Smith 1982) despite the unequal fitnesses of individuals adopting each tactic. Gross (1984) interpreted the reproductive strategy of maintaining dwarf and "normal" phenotypes in Arctic char populations (see Jonsson and Hindar 1982) as having evolved as a BBS.

The classical life history account of anadromous Atlantic salmon incorporates, and in large part depends upon, the implicit assumptions that (1) movement during juvenile stages is limited and infrequent prior to smoltification and (2) the young remain in a fluvial habitat throughout their freshwater phase of life (see Jones 1959; Scott and Crossman 1973). These are the precepts upon which Atlantic salmon production is estimated (but see Chadwick and Green 1985) and upon which life history models are based (e.g. Schaffer and Elson 1975). The present study suggests that the foregoing assumptions concerning parr movements may be inappropriate for anadromous salmon inhabiting systems containing lacustrine habitat. The importance of lakes to Atlantic salmon production in Newfoundland, and perhaps elsewhere, is a consideration which should be incorporated into current stream-oriented management practices.

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Statistical Properties of Alternative Parameterizations of the von Bertalanffy Growth Curve

D. A. Ratkowsky

CSIRO Division of Mathematics and Statistics, Tasmanian Regional Laboratory, Stowell Avenue, Hobart, Tasmania 7000, Australia

Ratkowsky, D. A. 1986. Statistical properties of alternative parameterizations of the von Bertalanffy growth curve. Can. J. Fish. Aquat. Sci. 43: 742–747.

The von Bertalanffy growth curve is often used in fisheries research to describe the relationship between the weight or length of a fish and its age. The equation is also encountered in various other branches of science and applied science in a variety of different parameterizations and names; for example, it is also known as the asymptotic regression equation or the three-parameter exponential equation. Since these equations are all nonlinear regression models, the properties of the least squares estimators of the parameters of these models may be very different from their large-sample properties, where the estimators are unbiased, have the minimum attainable variance, and are normally distributed, the conditions that pertain in a linear model. Different parameterizations will have estimators which approximate the asymptotic properties to varying degrees of closeness. My study of eight parameterizations shows that one of them, a generalization which allows unequal age increments of a parameterization proposed by Schnute and Fournier, is far superior to any of the other models, which include the most commonly used parameterization, in that it exhibits close-to-linear behavior. Two of the three parameters in this model represent the expected mean lengths corresponding to the youngest and oldest ages, respectively, in the sample, and thus have a ready biological interpretation. I discuss why it is important to have a close-to-linear model when one wishes to make comparisons between two or more data sets. Methodology is briefly described for carrying out such comparisons, and some further remarks are made about why biologists should be concerned about the statistical properties of the models that they use. Although most data sets I used for illustration are obtained from marine animals, the conclusions are general and apply to all disciplines which make use of the von Bertalanffy model in whichever guise or form it appears.

On utilise souvent la courbe de croissance de von Bertalanffy dans le cadre d'études sur les pêches afin de décrire le rapport entre le poids ou la longueur d'un poisson et son âge. Cette équation est également utilisée avec divers autres paramétrages et est connue sous divers noms dans d'autres domaines des sciences pures et appliquées. On l'appelle entre autres équation de régression asymptotique ou équation exponentielle à trois paramètres. Étant donné que ces équations sont toutes des modèles de régression non linéaire, les propriétés des estimations des paramètres de ces modèles (estimation par les moindres carrés) pourraient être très différentes des propriétés obtenues pour un grand échantillon, pour lequel les estimateurs ont un biais nul, une variance aussi faible que possible et une distribution normale, conditions qui reflètent un modèle linéaire. Les estimateurs de paramétrages divers se rapprocheront plus ou moins des propriétés asymptotiques. L'auteur a étudié huit paramétrages et a montré que pour l'un d'eux, une généralisation qui permet d'utiliser des incréments inégaux d'âges dans un paramétrage proposé par Schnute et Fournier est de loin supérieure à tout autre modèle, ce qui inclut les paramétrages les plus couramment utilisés du fait qu'ils présentent un comportement quasi-linéaire. Deux des trois paramètres de ce modèle représentent les longueurs moyennes prévues correspondant respectivement aux âges inférieurs et supérieurs de l'échantillon et peuvent donc être interprétés facilement dans un sens biologique. L'auteur explique ensuite pourquoi il est important que le modèle soit quasi-linéaire pour effectuer des comparaisons entre deux ou plusieurs ensembles de données. La méthodologie à utiliser dans ce cas est décrite brièvement et l'auteur explique en outre pourquoi les biologistes devraient connaître les propriétés statistiques des modèles dont ils se servent. Bien que la plupart des ensembles de données utilisés en exemple proviennent d'animaux marins, les conclusions sont générales et peuvent s'appliquer à tous les domaines qui utilisent déjà une forme ou une autre du modèle de von Bertalanffy.

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One of the most frequently used relationships in fisheries research to relate the length of a fish to its age is the von Bertalanffy growth curve (see Allen 1966; Phillips and Campbell 1968) in the following parameterization:

$$(1) \quad Y = L_\infty\{1 - \exp[-k(t - t_0)]\}$$

where Y is the length at time t, L_∞ represents the asymptotic length, t_0 is a constant defining the true origin of time, and k is a rate constant. Many other parameterizations of this model are also in use in applied science, for example:

$$(2) \quad Y = A - BC^t$$

where A, B, and C are constants. Equation (2) is said to be a "reparameterization" of (1) because the parameters A, B, and C in (2) may be expressed in terms of the parameters L_∞, k, and

t_0 of (1) exclusively, without involving the independent variable t. The relationship between the parameters of (2) and (1) is as follows:

$$A = L_\infty$$

$$B = L_\infty \exp(kt_0)$$

$$C = \exp(-k).$$

The same relationships also apply between the least-squares estimates of the parameters, that is, one merely replaces the parameters in the above expressions by their estimates.

Because parameterizations such as (1) and (2) are nonlinear regression equations, the statistical properties of the estimators of the parameters of one model may differ greatly from their properties in the other model. In linear regression models, under the assumption of an independent and identically distributed normal error term, the least-squares estimators of the parameters of the model are unbiased, normally distributed, and attain the minimum possible variance. For nonlinear regression models, this property holds only "asymptotically," that is, as the sample size goes to infinity. For smaller samples, such as may apply in real data sets, the estimators may be badly biased, non-normally distributed, typically having a long right-hand or left-hand tail, and have variances far in excess of the minimum possible variance. Different parameterizations of the same basic model may differ greatly in how closely the estimators approximate the asymptotic conditions. Thus, it is possible that one parameterization may give rise to estimators that deviate widely from the asymptotic properties, but another parameterization may have estimators that closely approximate those properties.

Earlier (Ratkowsky 1983) I argued in favor of nonlinear regression models whose least squares estimators come close to obeying the asymptotic properties, and termed such models "close-to-linear," since those properties prevail in linear regression models. Some of the benefits of a close-to-linear model include the fact that convergence to the least-squares estimates using the Gauss–Newton method should occur rapidly from any reasonable set of initial estimates. In contrast, a far-from-linear model may not converge unless one begins with initial estimates that are very close to the least-squares estimates. This consideration is particularly important when one has several sets of data for which one wishes to test for parameter invariance, that is, to test whether a parameter or parameters in the model have the same values in all data sets. This test is appropriately carried out using the "extra sum of squares" principle (Draper and Smith 1981), as I described in detail earlier (Ratkowsky 1983, Chap. 7). To perform this procedure, one must fit the model to each data set separately, and then fit the model to the combined data set, in which one or more parameters are to be estimated in common. Unless the parameterization of the model that is being used is close-to-linear, easy convergence is unlikely. Without convergence, the residual sum of squares cannot be calculated, and it is therefore not possible to do the test. Not only does use of a close-to-linear parameterization enable the estimates to be obtained readily, an additional benefit is that the predicted values of the response variate (length or weight) will be almost unbiased, that is, the assumption that the test statistic closely approximates an F-distribution will be valid and therefore the significance level obtained will be close to having that probability. The least-squares estimators of the set of parameters in a close-to-linear model will have joint confidence regions that are almost "ellipsoidal" in shape, and their almost total lack of bias means that one can make rough comparisons of their values between data sets by noting their magnitudes and standard errors in the different data sets. There is a natural temptation for scientists to make such comparisons, especially when one has produced a result which may be compared with values obtained by other workers. Of course, one should always remember that the appropriate correct test is via the extra sum of squares principle mentioned above. In a far-from-linear model, both the estimates and their standard errors may be grossly biased, so that even rough comparisons may lead to incorrect inferences.

A question that may be raised is whether a model that has good statistical properties in the sense described above necessarily has good biological interpretability. The relationship between the parameters of various parameterizations, such as those of (1) and (2), has already been given above. Even if one firmly believes that some biological interpretability has been sacrificed by resorting to a parameterization having good statistical properties but unclear biological meaning, the statistically suitable parameterization can still be used for parameter estimation and for carrying out appropriate tests, as discussed earlier. Conversion to the biologically more acceptable model can subsequently be made, since the least-squares estimates in any one parameterization are readily converted to the least-squares estimates in any other parameterization. However, the reader should not overlook the fact that the statistically poorer model will give rise to estimates having greater bias than those from a close-to-linear model. In any event, it will be seen that, of the parameterizations considered in this study, the one with the best statistical properties also has a ready biological interpretability.

Earlier (Ratkowsky 1983) I described a variety of measures and procedures for studying the estimation behavior of nonlinear models, which include the curvature measures of intrinsic (IN) and parameter-effects (PE) nonlinearity of Bates and Watts (1980), the bias measure of Box (1971), and the asymmetry measure of bias of R. K. Lowry. The value of IN measures the curvature of the "solution locus" in sample space, the locus representing all possible "solutions" to the estimation problem. In a linear regression model, the solution locus is straight, and IN is zero. In a nonlinear regression model, IN increases as the curvature increases, with the consequence being increased bias in the predicted values of the response variate Y and in the residual sum of squares. Reparameterization does not alter the shape of the solution locus; hence, all parameterizations have the same IN value for a given data set. PE measures the lack of parallelism and inequality of spacing of parameter lines on the solution locus (actually their projection on to the tangent plane at the solution locus). The value of PE is a single measure, being the maximum value of the parameter-effects curvature, obtained from a three-dimensional array called the "acceleration array." This array is really nothing more than a scaled version of the matrix of second derivatives of the regression model with respect to the parameters. In a linear regression model, the parameters appear linearly; hence, the second derivatives are all zero resulting in a PE value of zero. In a nonlinear regression model, the greater the departure of the model from linearity, the higher the value of PE. Unfortunately, the PE measure has sometimes been found (Ratkowsky 1983) to indicate a high degree of nonlinear behavior when other measures or simulation studies indicate close-to-linear behavior. Nevertheless, a low PE value is informative, and the goal of reparameterization should be to find a parame-

terization that makes PE as near to zero as possible. Although both Bates and Watts (1980) and I (Ratkowsky 1983) have used a test of significance to assess whether PE was "significant" or not, Healy (1984) has rightly pointed out that the use of a significance test is inappropriate, as the null hypothesis that the model is linear is known in advance to be false (i.e. a nonlinear model is obviously not a linear one). Nevertheless, values of $1/\sqrt{F}$, where F is drawn from a table of the F-distribution, which Bates and Watts (1980) view as the radius of curvature of a confidence region, may be regarded as "critical" values to serve as some guide to the extent of the nonlinearity, even if there is no formal significance test.

Box (1971) developed formulae for the bias in the least-squares estimates. Earlier (Ratkowsky 1983, p. 20–23) I used "percentage bias," that is, bias as a percentage of the estimate, but I noted that this quantity was not "location independent," and it was possible to obtain a high percentage bias merely because the estimate was near zero. Thus, although a high percentage bias often is truly indicative of bad estimation behavior, a simulation study is usually needed to check if the result is spurious.

Recently, Lowry and Morton (1983) developed an algebraic expression for the variance $\mathrm{Var}(\psi_i)$ of the asymmetry statistic ψ_i for the ith parameter described by Ratkowsky (1983, Section 2.9). There, the asymmetry statistic was defined as

$$\psi_i = [(\hat{\theta}_i^+ - \theta_i) + (\hat{\theta}_i^- - \theta_i)]/2$$

where $\hat{\theta}_i^+$ and $\hat{\theta}_i^-$ are the least-squares estimates obtained in a simulation trial after adding and subtracting, respectively, a vector of random errors to and from a hypothesized model. $\mathrm{Var}(\psi_i)$ was then written as an expression involving the variances of $\hat{\theta}_i^+$ and $\hat{\theta}_i^-$ and their covariance. The expression was then rearranged, and a formula for the correlation coefficient obtained, which varies from -1 to $+1$ (not 0 as erroneously stated in my book), with close-to-linear models producing values near -1. The value of the correlation coefficient had to be obtained from a simulation study because of the lack, at that time, of an algebraic expression for $\mathrm{Var}(\psi_i)$. Lowry and Morton (1983) have now filled in that gap by deriving the necessary expression for $\mathrm{Var}(\psi_i)$. Its computation requires knowledge of the formulae for the first and second derivatives of the model with respect of the parameters, the same quantities that are needed to calculate IN, PE, and the bias. Instead of using the correlation coefficient, Lowry and Morton employed the ratio $\lambda_i = \mathrm{Var}(\psi_i)/\mathrm{Var}(\hat{\theta}_i)$, where $\mathrm{Var}(\hat{\theta}_i)$ is the variance of $\hat{\theta}_i^+$ or $\hat{\theta}_i^-$ (the variances being identical). The ratio λ_i is termed the asymmetry measure of nonlinearity, and has values between 0 and 1. Extensive use of this measure by myself has shown that if $\lambda_i < 0.01$, the estimator is close-to-linear, but larger values generally indicate increasing skewness in the distribution of the estimator. If $\lambda_i > 0.05$, the skewness is very perceptible if histograms of the estimates are drawn after carrying out a simulation study. Unlike the percentage bias measure based on the formula of Box (1971), λ_i is location (as well as scale) independent; thus, high values truly indicate far-from-linear behavior.

The Models

A total of eight different parameterizations of the von Bertalanffy equation was studied. These parameterizations were selected because these are either the ones in use in practice, or have been proposed for practical use, or were deemed to be worthy of study for other reasons. As there are an infinite number of reparameterizations, there is no guarantee that the "best" of these is best in any global sense. The models were as follows:

$$(3)\quad Y = \mathrm{ASYMP}\,\{1 - \exp[-K(X - t_0)]\}$$

$$(4)\quad Y = \mathrm{ASYMP} - \mathrm{RANGE}\cdot\gamma^X$$

$$(5)\quad Y = \mathrm{ASYMP} - \mathrm{RANGE}\cdot\exp(-KX)$$

$$(6)\quad Y = \mathrm{ASYMP} + (\mathrm{INT} - \mathrm{ASYMP})\,\gamma^X$$

$$(7)\quad Y = \mathrm{ASYMP} + (\mathrm{INT} - \mathrm{ASYMP})\exp(-KX)$$

$$(8)\quad Y = \mathrm{ASYMP} - \exp[-(\mathrm{LOGRANGE} + KX)]$$

$$(9)\quad Y = \mathrm{INT} + \mathrm{RANGE} - \mathrm{RANGE}\cdot\exp(-KX)$$

$$(10)\quad Y = l + (L - l)\,\frac{1 - k^{m-1}}{1 - k^{n-1}}$$

where $m = 1 + (n-1)\,[(X - X_1)/(X_n - X_1)]$, n is the number of data points, and the values of X are arranged in ascending order so that X_1 is the lowest (usually time or age) and X_n is the highest. Symbols or names that are the same in different models have the same meaning (and the same least-squares estimates). Thus, ASYMP represents the Y-asymptote in each of (3)–(8), INT is the intercept on the Y-axis (i.e. the Y value when $X = 0$), RANGE = ASYMP − INT is the range, and LOGRANGE is the logarithm of the range. The parameters γ and K relate to the rate at which Y changes from its initial value INT to its final value ASYMP. In (3), t_0 represents the "true" origin of time. In (10), l is the expected value of the response at the earliest observed time X_1, L is the expected value at the final observed time X_n, and k is comparable with γ (and equal to it when the X values represent equally spaced annual data). Model (10) is a generalization of the parameterization proposed by Schnute and Fournier (1980) in which m was restricted to the values 1, 2, . . . , n, and thus was suited only to equally spaced X values representing age-classes separated by exactly 1 yr. The generalization given by the expression for m in (10) is completely unrestricted while still collapsing to the Schnute–Fournier model for annual data.

Data Sets

Six data sets were studied, the first four of which involve the relationship between size, as measured by length or weight, and age of fish or marine mammals. The remaining two sets of data are included to test the generality of the results, to see whether the same conclusions apply to data obtained from other disciplines. The data sets are as follows, where n is the sample size: (1) total length of pacific herring (*Clupea harengus pallasi*) vs. age (n = 13; see Gulland 1969, p. 41; (2) weight of shark (*Mustelus kanekonis*) vs. age group (n = 4; see Gulland 1969, p. 42); (3) length of dugong (*Dugong dugon*) vs. age (n = 27; see Ratkowsky 1983, p. 101); (4) length of perch (*Roccus americanus*) vs. age (n = 9; see Krueger 1962, p. 454); (5) leaf production vs. irradiance (n = 6; see Ratkowsky 1983, p. 102); (6) turkey weights vs. amount of methionine supplementation (n = 35; see Noll et al. 1984; original data supplied courtesy of Dr. J. A. Witmer).

Results and Discussion

Results of the assessment of statistical properties of (3)–(10) are given in Tables 1 and 2. Table 1 presents the values of the

TABLE 1. Intrinsic (IN) and parameter-effects (PE) nonlinearities of Bates and Watts (1980).

Data set	IN (all models)	PE (3)	PE (4), (6)	PE (5), (7), (9)	PE (8)	PE (10)	"Critical" value $(1/\sqrt{F})$
(1) Herring	0.067	2.76	0.90	1.05	1.11	0.07	0.52
(2) Shark	0.020	10.42	11.29	12.54	18.20	0.06	0.07
(3) Dugong	0.207	4.18	1.41	1.53	1.54	0.79	0.58
(4) Perch	0.088	8.23	5.48	6.05	6.61	0.14	0.46
(5) Leaf	0.232	2.56	1.53	1.54	1.54	0.23	0.33
(6) Turkey	0.141	2.76	3.49	1.14	1.20	0.35	0.59

TABLE 2. Lowry–Morton λ values.

Data set	ASYMP	INT	RANGE	LOGRANGE	t_0	γ	K	l	L	k
(1) Herring	0.015	0.006	0.019	0.015	0.010	0.002	0.003	0.001	0.001	0.002
(2) Shark	0.043	0.001	0.052	0.029	0.002	0.001	0.000	0.000	0.000	0.001
(3) Dugong	0.033	0.014	0.047	0.049	0.035	0.026	0.030	0.006	0.015	0.026
(4) Perch	0.089	0.004	0.151	0.124	0.026	0.004	0.004	0.001	0.002	0.004
(5) Leaf	0.067	0.024	0.105	0.106	0.053	0.028	0.029	0.007	0.010	0.022
(6) Turkey	0.029	0.001	0.028	0.025	0.027	0.382	0.014	0.001	0.004	0.013

IN and PE values of Bates and Watts (1980). IN is the same for all parameterizations, but in general PE is different for each model. However (and this points to a further weakness of the PE measure, in addition to its tendency to sometimes apparently overstate the extent of nonlinearity), since PE examines all linear combinations of the parameters in order to find the maximum curvature, any model whose parameters are linear combinations of the parameters in some other model will have the same PE value as that model. For this reason, (4) and (6) have the same PE values, as do (5), (7), and (9) in Table 1. As mentioned in the introduction to this paper, a test of significance for either IN or PE may be seen to be inappropriate. Nevertheless, values of $1/\sqrt{F}$, where F is drawn from a table of the F-distribution with numerator degrees of freedom equal to the number of parameters and denominator degrees of freedom equal to the residual degrees of freedom, are given in the last column of Table 1. Using these "critical" values as guides to the extent of the nonlinearity, it is seen that for each data set, IN is less than this value, whereas for all data sets the PE values for all models exceed these values, except for (10), where PE is less than the critical value for all data sets except the dugong data set. This is a clear indication that (10) has a lower departure from linear behavior than any other model.

Table 2 presents values of the Lowry and Morton (1983) λ values for each parameter for each data set. Only the parameter l has all its λ values less than 0.01, but several parameters (INT, K, l, L, k) have all λ values less than 0.05, beyond which perceptible skewness may be expected. The parameters l, L, and k all belong to model (10), and for three of the data sets, all λ values for these parameters are less than 0.01. No other model has its three parameters consistently as well-behaved as this. For example, (3)–(8) all contain parameter ASYMP, which never has λ values less than 0.01, and for two data sets λ exceeds 0.05. Previously (Ratkowsky 1983, Chap. 5), I examined some parameterizations of this parameter by replacing it in the formulae in which it appears by (i) its reciprocal and (ii) its exponential, but in each case this resulted only in a marginal improvement in behavior. Model (9) dispenses with parameter ASYMP, but as parameter RANGE, which appears in its place, is no better behaved, the model offers no improvement over those containing ASYMP. Model (10) is a completely different concept from the other models considered here in that the parameters of that model do not include "extrapolated" values such as the asymptote, intercept, or range, all of which depend on estimation outside the range of the observed X values. Model (10) contains "expected value" parameters such as advocated by Ross (1970), since l and L are each expected values of the response variable Y for particular X values. Ross (1970) argued in favor of expected value parameterizations on the grounds that the parameters so obtained were likely to be less correlated than the parameters in other parameterizations. I have already shown (Ratkowsky 1983, p. 191–196) that there is no connection between parameter correlation and the behavior of the least-squares estimator. Whether or not a set of estimators of nonlinear regression parameters exhibits close-to-linear behavior is related to how closely those estimates are to having a joint normal distribution. It is of no consequence whether the correlation between parameters is high or low (unless the correlations are so high that there may be problems in matrix inversion using a computer), as the statistical properties of the estimators including their biases, covariances, skewness, and kurtosis coefficients do not depend upon correlation. Table 3 presents the correlation coefficient between parameters L and k in (10), this parameter pair having the largest correlation of the three parameter pairs in that model, and the correlation coefficient between ASYMP and K in (7), this parameter pair having the largest correlation of the three parameter pairs in that model. Table 3

TABLE 3. Maximum correlation coefficients between parameter pairs in models (10) and (7).

Data set	Correlation between L and k in (10)	Correlation between ASYMP and K in (7)
(1) Herring	0.710	−0.932
(2) Shark	0.551	−0.997
(3) Dugong	0.827	−0.878
(4) Perch	0.687	−0.982
(5) Leaf	0.631	−0.835
(6) Turkey	0.681	−0.852

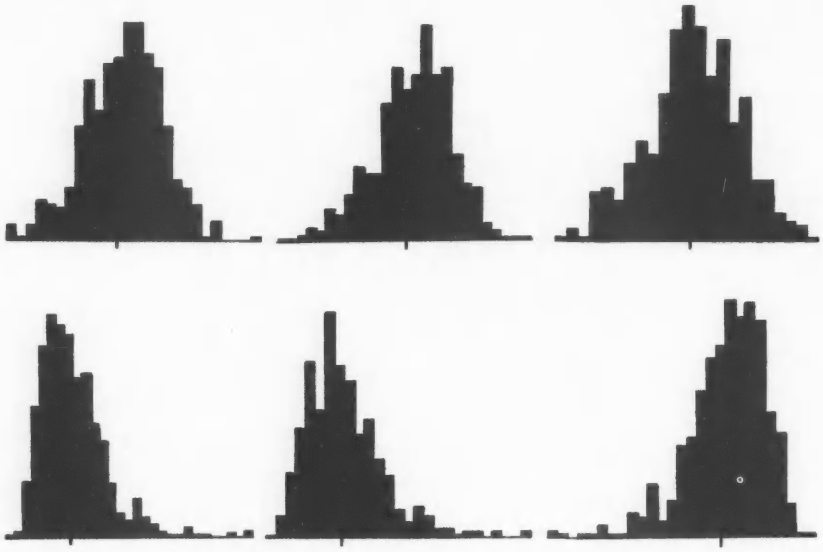

FIG. 1. Histograms from a simulation study on the perch data (data set (4)). Top row, left to right: estimates of l, L, and k, respectively. Bottom row, left to right: estimates of ASYMP, RANGE, and LOGRANGE, respectively. The vertical axes represent the observed frequency for each of the classes.

shows that, although for each data set the correlation is lower in absolute magnitude in (10) than in (7), these coefficients are still substantial in size and thus a long way from indicating "independence" of the estimators.

The various measures of nonlinearity in Tables 1 and 2 indicate that model (10) is by far the best behaved parameterization of those studied. To test the validity of this conclusion, simulation studies were carried out for data sets (1)–(4), those involving marine animals. In each case, 500 pseudo-random data sets were created in a similar fashion to the procedure I previously described (Ratkowsky 1983, Section 2.6). The 500 data sets that were generated were fitted by model (10), since that model behaves close-to-linear and thereby would likely insure that convergence would occur in each data set using the assumed "true" values of the parameters as initial estimates. Once the least-squares estimates for (10) were obtained, the estimates of the parameters in the other models were obtained by direct transformation. For example, the relationships between the parameters of (10) and the parameters of (3) are as follows:

$$\text{ASYMP} = \frac{L - lk^{n-1}}{1 - k^{n-1}}$$

$$K = \frac{-(n-1)}{(X_n - X_1)} \log k$$

$$t_0 = X_1 - \frac{(X_n - X_1)}{(n-1)\log k} \log\left\{\frac{L - l}{L - lk^{n-1}}\right\}.$$

(The expressions for K and t_0 differ slightly from equations (9) and (10) of Schnute and Fournier (1980) because they considered age-classes separated by 1-yr intervals. That restriction results in the term $X_n - X_1$ having the same value as $n - 1$, thereby cancelling out those terms in the latter two equations.)

The simulation studies gave results in accordance with the conclusions drawn from the Lowry–Morton λ values. In every case where the Lowry–Morton λ values exceeded 0.05, the distribution of the 500 estimated values of the corresponding parameter was highly biased and skewed. Wherever λ was less than 0.01, the distribution of the estimates was close to that of a normal distribution. For example, Fig. 1 presents results for the estimates of l, L, and k in (10) and for the estimates of ASYMP, RANGE, and LOGRANGE appearing in other models for the data on perch (data set (4)). The distribution of the estimates of the parameters in (10) are indistinguishable from that of a normal distribution, whereas the distribution of ASYMP, RANGE, and LORANGE all exhibit clear visual departures from normality. The consistency of the results obtained from the four data sets, despite the fact that one data set (set (2)) has only four data points, suggests that the conclusions may enjoy general validity and not be confined only to the data sets considered here.

A further test of the generality of the conclusion that model (10) is the best from the statistical point of view was made by examining a number of other data sets. These include data for height versus age for forest species from sample plots in British Columbia and for the growth of bird nestlings. In all cases, (10) exhibited close-to-linear behavior. Thus, this parameterization appears to be the most suitable one to use of all the models studied to date. Of course, this does not necessarily mean that some other parameterization, as yet unstudied, may not be better yet. However, as the PE values for (10) were always less than 1.0, usually much less, there is very little room for improvement.

Model (10) should find acceptability on biological grounds from users of the von Bertalanffy equation. In the fisheries context, Schnute and Fournier (1980) pointed out that the biologist actually knows both the shortest and longest observed lengths (where length is the response variable). These may be used as initial estimates of l and L, respectively. An initial estimate of k may be obtained by the trial-and-error method suggested by Schnute and Fournier (1980). However, I have found that, because (10) is close-to-linear in behavior, con-

vergence occurred in all data sets that I tested from initial values that were remote from the converged values of the least-squares estimates. Hence, the choice of initial value is not critical. Model (10) is also very amenable to making comparisons between several sets of data, especially if the minimum and maximum ages are the same in each data set. Then, a test of the invariance of l and/or L becomes a test as to whether the mean lengths at the extreme ages are the same or not between the several sets of data. This does indeed seem a more realistic approach, from the biological point of view, than the alternative of testing parameters such as ASYMP, INT, or t_0, all of which represent extrapolations outside the range of the data. Thus, as Schnute and Fournier (1980) suggested, the parameters l, L, and k may have greater validity biologically than those in any of the other parameterizations considered, since the formulae of the others all contain at least one parameter representing an extrapolation outside the observed range of the data.

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Recruitment Variability and Its Implication for Managing and Rebuilding the Georges Bank Haddock (*Melanogrammus aeglefinus*) Stock

William J. Overholtz, Michael P. Sissenwine, and Stephen H. Clark

National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole Laboratory, Woods Hole, MA 02543, USA

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The Georges Bank haddock (*Melanogrammus aeglefinus*) fishery has fluctuated dramatically since the early 1960's. Abundance declined from the mid-1960's to the mid-1970's, partially recovered, and has declined again since 1980. In general, poor year-classes have been associated with a low spawning biomass although the relationship is variable. The fishery was simulated by using the Baranov catch equation, constant growth and natural mortality, and stochastic levels of recruitment whose probabilities correspond to historic patterns in the stock and recruitment data. Simulations suggest a low probability for stock recovery and improved yield under current conditions ($F \approx 0.5$). Recovery time increased with increases in fishing mortality (F), and beyond $F = 0.40$ recovery is unlikely within 25 yr. With recruitment of a very large year-class (100 million fish) an initial strategy providing for a relatively low level of $F(= 0.10)$ for 3–5 yr, followed by exploitation at historically sustainable levels ($F = 0.35$), would result in stock recovery. With recruitment of a smaller year-class (50 million fish) low initial levels ($F = 0.10$) and subsequent management at or near $F_{0.1}$ ($F = 0.26$) would be required to initiate stock recovery and reasonable harvest levels in future years.

Dans la région du Banc Georges, la pêche de l'aiglefin (*Melanogrammus aeglefinus*) fluctue dramatiquement depuis le début des années 1960. Du point de vue de son abondance, cette espèce a décliné du milieu des années 60 au milieu des années 70, puis a partiellement récupéré, et a de nouveau décliné à partir des années 80. En général, on a associé les classes annuelles faibles en nombre à une biomasse caractérisée par un faible taux de reproduction, bien que la relation soit variable. On a simulé les pêches en utilisant l'équation de Baranov relative à la prise, les taux de croissance continue et de mortalité naturelle, à des niveaux stochastiques de recrutement dont les probabilités correspondent à l'évolution historique du stock et du recrutement, indiquée par les données. Les simulations suggèrent une faible probabilité de régénération des stocks et d'amélioration du rendement dans les conditions actuelles ($F \approx 0{,}5$). Le temps de régénération augmente de façon proportionnelle à la mortalité survenant durant la pêche (F), et au-delà de $F = 0{,}40$, toute récupération est improbable en moins de 25 ans. En recrutant une classe annuelle très vaste (100 millions de poissons) et en adoptant une stratégie initiale prévoyant un niveau relativement bas de $F(= 0{,}10)$ pendant 3 à 5 ans, suivie de l'exploitation à des taux historiquement soutenables ($F = 0{,}35$), on permettrait une régénération des stocks. Avec le recrutement d'une classe annuelle plus petite (50 millions de poissons), il faudrait des taux initiaux bas ($F = 0{,}10$) et une gestion ultérieure à $F_{0.1}$ ou près de $F_{0.1}$ ($F = 0{,}26$) pour amorcer une régénération des stocks et espérer des niveaux raisonnables de récolte dans les années à venir.

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Haddock (*Melanogrammus aeglefinus*) are widely distributed in the western North Atlantic, where at least seven separate stocks have been recognized (Grosslein 1962). On Georges Bank (located to the east of Massachusetts) haddock have been fished intensively since the early 1900's and the subject of research efforts since 1931. Stock abundance has fluctuated greatly since 1960, a period when landings and stock biomass (age 2 and older) had averaged 46 000 and 153 000 t, respectively (Clark et al. 1982). Biomass increased in the early to mid-1960's due to strong recruitment (Fig. 1) and international landings rose dramatically; decreases in stock biomass and recruitment followed. The late 1960's and early to mid-1970's were characterized by low stock biomass and poor recruitment. Some recovery occurred in the late 1970's and early 1980's, but in succeeding years recruitment has again been poor and abundance has declined (Fig. 1) (Overholtz et al. 1983).

The relationship between recruitment and parental stock size has been the subject of numerous research papers. Ricker (1963) demonstrated the importance of spawning biomass in relation to harvest levels. Goodyear and Christensen (1984) examined spawning stock size and recruitment interrelationships where year-class size was strongly dependent on environmental factors and concluded that lack of a firm empirical relationship was not proof that recruitment was independent of stock size, suggesting that some baseline level of spawning stock should be preserved. Kruse (1983) showed that both spawning stock biomass and environmental influences were important components of a recruitment model of an English sole (*Parophrys vetulus*) stock, even though no clear stock–

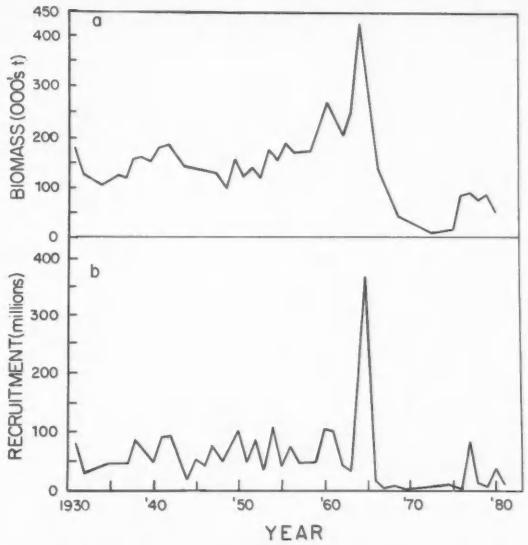

FIG. 1. Georges Bank haddock (a) stock sizes 100% age 2 and older and (b) age 2 recruitment for 1931–81.

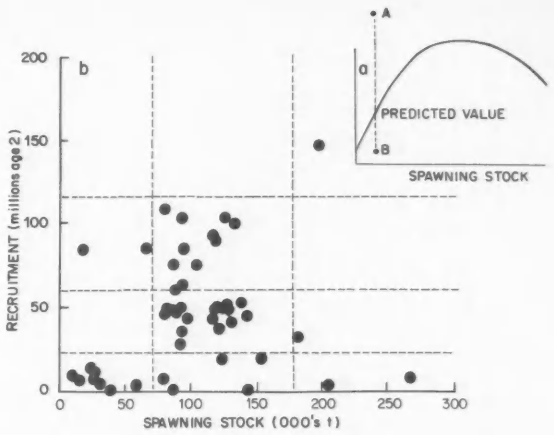

FIG. 2. (a) Hypothetical stock–recruitment curve with predicted value and possible observed values for a particular stock size. (b) Spawning stock biomass (age 3 and older) and subsequent recruitment (age 2) for Georges Bank haddock, 1931–79. The 1963 point (194 700 t and 368.8 million recruits) has been omitted.

recruit relationship existed.

Recent studies showed that when spawning stock biomass (age 3 and older) ranged from 70 000 to 200 000 t, recruitment averaged 61 million fish and an above-average year-class (>60 million fish) occurred about once every 3 yr for Georges Bank haddock (Fig. 2b) (Clark et al. 1981, 1982; Overholtz et al. 1983). When biomass was below this range, however, poor year-classes resulted in every year except 1975. A pattern of low biomass producing poor recruitment developed during 1966–74 (Fig. 1b) and was repeated during 1981–84 (unpublished data). When the 1975 year-class matured, spawning stock biomass reached 90 000 t and another relatively good year-class was produced in 1978. Also, production of prerecruit haddock in 1980 was higher than in most recent years.

This study utilizes recruitment and parent stock data to construct a stochastic simulation model to examine the long-term effects of fishing on the recovery of the spawning stock. Alternative strategies for rebuilding the stock were also studied by simulating recruitment of good year-classes and applying various target levels of fishing mortality over a long period.

Model Background and Strategy

Deterministic models have not been useful for modeling the haddock stock–recruitment problem because of failure to reproduce the variability that occurs over the full range of parental stock sizes, for instance, the above (*A*) or below (*B*) average recruitment (Fig. 2a) that occurs at the lower end of the parental stock scale. Application of these models has resulted in poor correlations and little variation explained (Grosslein and Hennemuth 1973; Clark et al. 1982).

Although there is not a useful empirical relationship between spawning stock and recruitment, there do appear to be some stock-related influences. A recent analysis suggests that current levels of spawning stock biomass per recruit are inadequate to maintain the stock and suggests that there is little chance for rebuilding (Gabriel et al. 1984). The probability of producing a good year-class has been on the order of 10% recently when the spawning stock was relatively low (Fig. 2b). At present, stock abundance can be projected about 2 yr in advance, but a longer-term perspective would be useful for studying future management options.

Since deterministic methods have proved to be less than adequate for this purpose, we chose a stochastic method that provides a technical solution to the stock–recruitment problem. The method allows for the transformation of stock–recruitment information into a probability transition matrix which can then be used in a variety of ways to simulate recruitment. The original application by Getz and Swatzman (1981) addressed the problem of modeling yellowtail flounder (*Limanda ferruginea*), haddock, and South African anchovy (*Engraulis capensis*) fisheries. It was subsequently used to provide advice for the management of Pacific whiting (*Merluccius productus*) (Swartzman et al. 1983).

Recruitment was generated from stock biomass using a probability schedule following procedures used by Getz and Swartzman (1981). Data were divided into cells which represented natural breaks or clusters of observations (Fig. 2b). Two stochastic events determined recruitment at a particular stock size of interest. The first determined which vertical cell was chosen by assigning a probability range to each region based on the number of observations in each cell; the second determined which level of recruitment would result from the possible range of choices in that particular cell (Fig. 2b). This method provides a solution to the problem of defining stock–recruit relationships in fish populations in which enough data are available to determine transition probabilities. The Getz–Swartzman method is more useful than attempting to fit a hypothetical curve through uncorrelated data, since it is not subject to problems such as inappropriate model choice, or poor fits to the data. It also removes or ignores autocorrelation which can become a problem in some cases (Sissenwine 1977a).

The rest of the model was organized in a fashion similar to many common fishery models (Walters 1969; Sissenwine 1977b). The Baranov catch equation was used to calculate

annual yields, and age-specific year-class size was estimated (up to a maximum age of 10) using survival rates from the negative exponential relationship (Beverton and Holt 1957). Natural mortality was assumed equal to 0.2 as in previous studies (Clark et al. 1982). Fish were assumed to recruit to the fishery at age 2 and to the spawning stock at age 3 (Clark et al. 1982; Overholtz et al. 1983). Growth at age was assumed to follow an average pattern, since recent data suggest that it has changed little since 1977.

The model was designed so that population response to different F levels could be studied. At each level used (0.10, 0.26[1], 0.40, 0.55[2], 0.70), 40 runs of 25-yr duration were performed for a total of 1000 simulated recruitment values. Each of the simulated data points were averaged over their particular year of occurrence and a 25-yr trend for each F level was produced. To start each simulation, stock size was assumed equal to 1983 levels, when biomass was at or near historic low levels (Overholtz et al. 1983). The initial stock estimates were determined from a modified DeLury method that utilizes age-specific catch per tow indices from research cruises and commercial catch at age in numbers (Collie and Sissenwine 1983). A spawning stock of 70 000 t was chosen as a reference level that best corresponded to a rebuilt stock as determined from stock data in Fig. 2b. Rebuilding times were calculated for all runs at each F level to provide an estimate of the time required for rebuilding the spawning stock. While this approach provides a useful perspective in relation to spawning biomass, it does not account for other potentially important characteristics, such as age structure and age-specific fecundity and egg viability.

Simulation Results

Yield and Biomass Levels

Not surprisingly, results of this study suggest that fishing mortality will play a major role in determining the future status of this stock (Fig. 3). Reductions in F resulted in improved recruitment and increased spawning stock biomass and yield. If F is 0.40 or greater, then spawning biomass (ages 3 and older) will not recover (Fig. 3a). Spawning stock biomass recovers most rapidly under low F levels, reaching 250 000 and 140 000 t on average at $F = 0.0$ and 0.10, respectively (Fig. 3a). Recovery occurs because recruitment exceeds catch and natural mortality on average and the stock is always more than replacing itself. Production of an above-average year-class under such conditions will result in rapid increases in spawning stock size. Long-term average simulated yield ranges from 11 000 to 15 000 t if F is 0.40–0.70 (Fig. 3b). At lower F values (0.10, 0.26, yields would initially be smaller, but would eventually surpass those from higher F options (Fig. 3b).

The reasons for these responses become obvious when recruitment levels generated by these simulations are examined. Stock rebuilding occurs when $F \leq 0.26$ (Fig. 4) because the frequency and magnitude of good year-classes increase. At higher levels of F, recruitment is inadequate for stock rebuilding and spawning stock biomass remains low.

The range of recruitment is also much greater at lower F levels ($F = 0.00$, 0.10, 0.26, see Fig. 4). In the absence of fishing, recruitment ranged from 0 to 360 million fish and 0 to

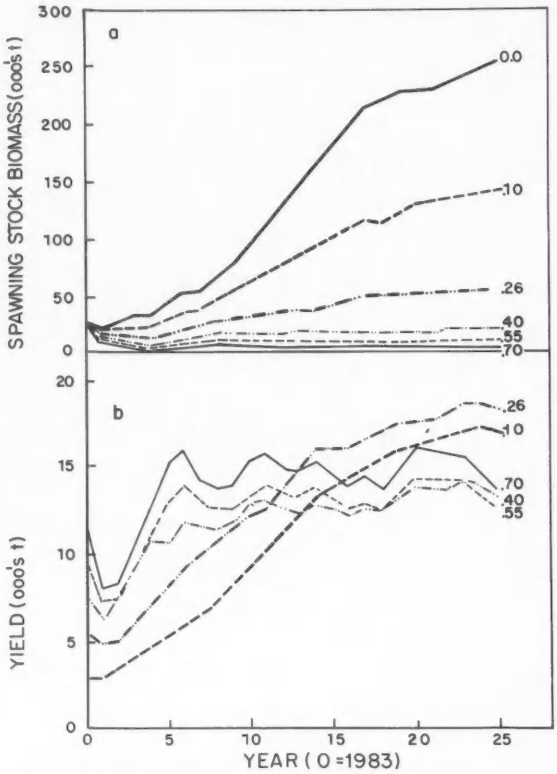

FIG. 3. (a) Predicted spawning stock and (b) yield from simulations under six fishing mortality options ($F = 0.00$, 0.10, 0.26, 0.40, 0.55, 0.70) for forty 25-yr runs for the Georges Bank haddock stock.

340 million fish at F levels of 0.10 and 0.26. The range in recruitment declined considerably at F levels greater than 0.40 and hovered between 0 and 80 million fish at $F = 0.55$ and $F = 0.70$. This measure of the magnitude of recruitment reflects the frequency that the stock is $\geq 70\,000$ t, a region of S–R space where past performance shows that recruitment will be much higher on average (Fig. 2b).

Rebuilding Times

The simulation model was also used to investigate stock rebuilding times under different F levels. As would be expected, average rebuilding times increase as F increases (Fig. 5). The average time required ranged from 11 yr at $F = 0.00$ to 19.3 yr at $F = 0.40$ for runs in which recovery occurred, and at higher F levels ($F = 0.55$, 0.70) recovery was not possible, at least over a 25-yr time span. The probabilities of recovery also suggest that only low fishing mortalities will result in rebuilding (Fig. 5).

The percent frequency of various spawning stock levels, determined as the number of times the stock size met or exceeded the specified level in 40 runs, under different fishing options was also investigated. The spawning stock was maintained at 70 000 t or greater for 60% of the time if the stock is not fished ($F = 0.0$) or 43% if lightly fished ($F = 0.10$) (Fig. 6). The frequency of stock sizes of 90 000 or 150 000 t is also reasonably high under these F options.

[1] $F_{0.1}$ (Clark and Overholtz 1979).
[2] F_{max} (Clark and Overholtz 1979).

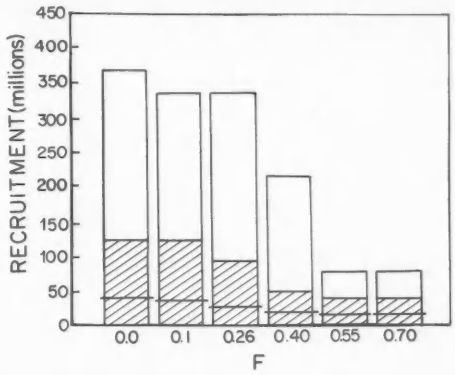

FIG. 4. Mean recruitment and 95% confidence intervals (cross-hatched area) and range of recruitment (0 to top of bar) from simulations under six fishing mortality options (F = 0.0, 0.10, 0.26, 0.40, 0.55, 0.70) for forty 25-yr runs for the Georges Bank haddock stock.

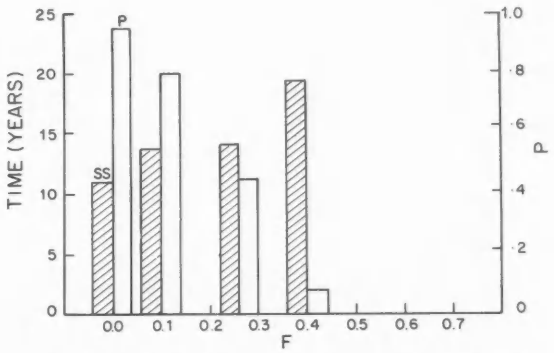

FIG. 5. Calculated rebuilding times for the spawning stock (SS) and probability (P) that SS will recover in the calculated time frame under six fishing mortality options (F = 0.00, 0.10, 0.26, 0.40, 0.55, 0.70) for forty 25-yr runs for the Georges Bank haddock stock.

Rebuilding Strategies

We investigated management strategies for stock rebuilding under different recruitment levels. The information in Fig. 3 suggests that even when recruitment levels are generally poor the stock would begin to increase gradually at low F levels. An appropriate rebuilding strategy might therefore be to lower F to protect a large year-class for a reasonable amount of time. Then fishing mortality rates could be set to a level that produced reasonable yields in the past.

To investigate this management strategy the model was run for two recruiting year-class size options and several F levels. Fifty million and 100 million fish were chosen as appropriate cohort sizes corresponding to moderate and large year-classes in the past; forty 25-yr simulations were averaged for each option. In addition, control simulations with F held at a constant level were produced to measure the effectiveness of the strategy. Results indicate that if the stock is fished at F = 0.10 for the first 5 yr and F = 0.35 thereafter, the spawning stock recovers quickly and declines gradually to about 80 000 t under the 100 million fish option (Fig. 7a). The 50 million fish option, however, produces a situation where recovery occurs

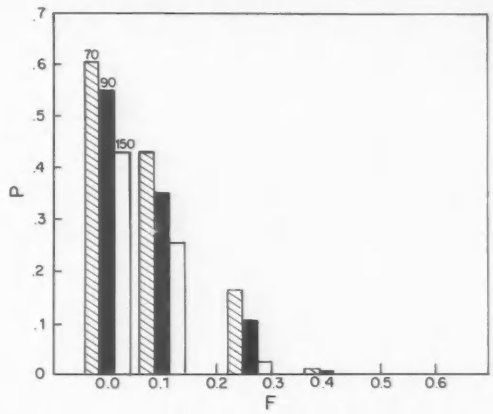

FIG. 6. Frequency distribution of the number of occurrences (proportion of the time (P)) that the spawning stock was at or above (70 000, 90 000, and 150 000 t) under six fishing mortality options (F = 0.00, 0.10, 0.26, 0.40, 0.55, 0.70) for forty 25-yr runs for the Georges Bank haddock stock.

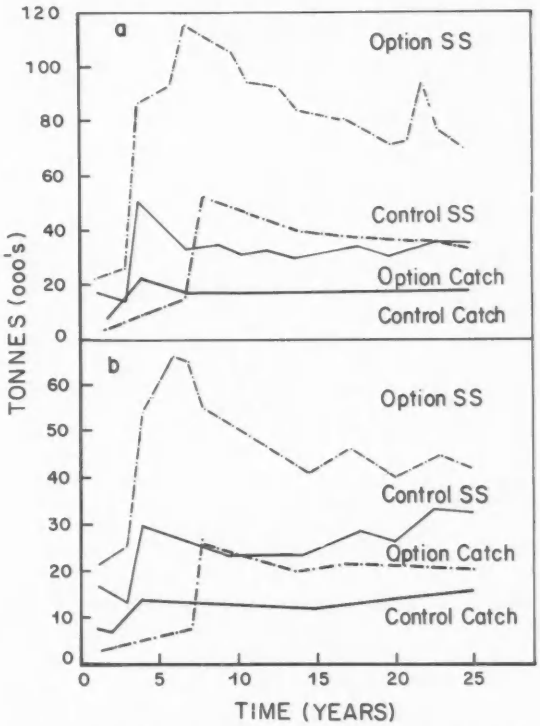

FIG. 7. Simulated yield (Option Catch) and spawning stock size (Option SS) for two levels of initial year-class ((a) 100 million and (b) 50 million) under a fishing mortality schedule of F = 0.10 for the first 5 yr after recruitment and F = 0.35 for the next 18 yr for the Georges Bank haddock stock. Control runs (Control Catch and SS) with F = 0.35 over all years are included for comparison.

rapidly, but spawning stock declines after the initiation of fishing at F = 0.35 (Fig. 7b). Long-term yields from these two strategies would be considerably different. The first option would yield about 40 000 t, something close to the long-term

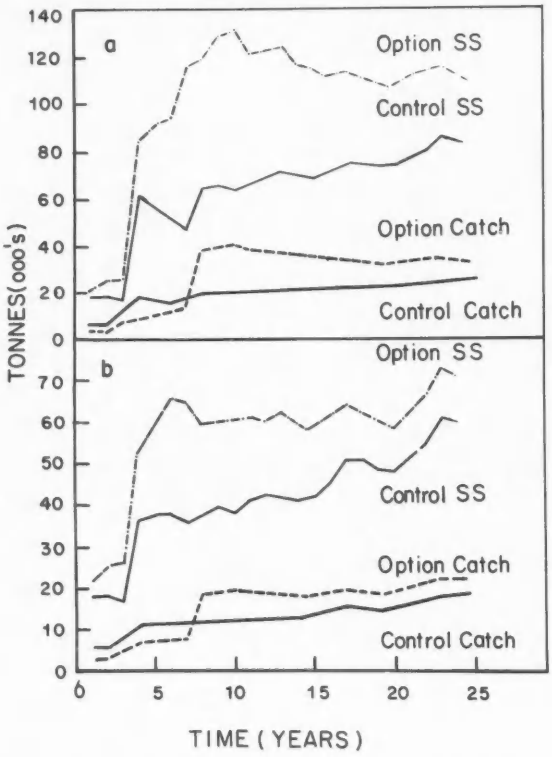

FIG. 8. Simulated yield (Option Catch) and spawning stock size (Option SS) for two levels of initial year-class size ((a) 100 million and (b) 50 million) under a fishing mortality schedule of $F = 0.10$ for the first 5 yr and $F = 0.26$ for the next 18 yr for the Georges Bank haddock stock. Control (Control Catch and SS) runs with $F = 0.26$ over all years are included for comparison.

average for this stock, while the second would yield slightly over 20 000 t. In both cases the protection strategy produces larger yields and spawning stocks than the constant F strategy (Fig. 7).

Another alternative would be to follow the same strategy of protecting the year-class initially and then applying a lower level ($< F = 0.35$) of fishing mortality). Management of a fishery at a level consistent with a conservative approach suggests that an $F_{0.1}$ strategy would be appropriate. We made another set of runs in which the two year-class options were fished at a rate of $F = 0.26$, the $F_{0.1}$ level for the Georges Bank haddock stock. Under the 100 million fish option the spawning stock again recovered rapidly and remained at roughly 120 000 t (Fig. 8a). Long-term yield declined slightly to about 38 000 t. Under the 50 million fish alternative the spawning stock stabilized at a much higher level than in the previous strategy (Fig. 8b). Yield also averaged about 20 000 t under this option. Again, the protection strategy was better than the control option, especially for the 100 million fish option (Fig. 8a).

Other applications of F applied over different time intervals yielded similar results. For instance, when the 50 million fish option was lightly exploited for 10 yr and then fished at $F = 0.35$, spawning stock biomass still declined.

One potential problem with these simulations and the Getz–Swatzman approach is whether choice of cutoff points for the stock–recruitment transition data unduly influences the outcome of the simulations. For instance, the 70 000 t level may have been too high (Fig. 2b). In addition, there is a paucity of data points between 40 000 and 70 000 t. The question arises as to whether an artificial barrier is being created by the somewhat arbitrary decision of where to place the cutoff point for the next stock–recruit transition cell.

To investigate the sensitivity of the model to this issue the transition stock size was varied such that the spawning stock necessary to move into the next probability region was made successively smaller. The results of these additional simulations suggest that the model results were not overly influenced by this problem. In fact, it was only when the transition stock level was moved into the 20 000 to 30 000 t range, the area where recruitment has consistently failed in the past (Fig. 2b), that the 50 million fish option provided enough recruitment to allow a fishery at $F = 0.35$ and recovery of the spawning stock. The model therefore behaved reasonably well and the chosen probability cells were appropriate.

Discussion

The term "recruitment overfishing" implies exploitation of a fishery resource at such an intensive level that compensatory stock responses are insufficient to maintain a normal pattern of recruitment. That is, the expected situation where moderate to good year-classes are produced each year is replaced by a cycle where poor year-classes become common, moderate to good ones become rare, and stock dynamics are much more variable. Cushing (1977) defined it as occurring when year-class size falls well below the expected recruitment that occurs at high adult stock sizes.

Recruitment has failed in many North Atlantic haddock stocks following overexploitation (Sahrage and Wagner 1978; Templeman et al. 1978; Templeman and Bishop 1979; Clark et al. 1982); the Georges Bank haddock stock is one example. Recruitment failed in the mid-1960's and good year-classes have been rare. Presumably, recruitment prospects would be enhanced if spawning biomass were allowed to rebuild to a level where the probability of producing good year-classes is increased.

When the normal recruitment pattern for a fish stock is disrupted, the fishery for that species can collapse rapidly and it may take years for a stock to rebuild with no certainty of when recovery will occur (Archibald et al. 1983). Two productive Northwest Atlantic haddock stocks off the coast of Newfoundland were heavily exploited in the 1950's and early 1960's by an international fishery, collapsed, and still have not recovered (Templeman et al. 1978; Templeman and Bishop 1979). Years of economic disruption and loss of management options follow such commercial extinctions. That some good year-classes have been produced from stock sizes near current levels suggests that Georges Bank haddock can recover.

Our study suggests that restoration of the Georges Bank haddock stock to former levels of yield will be contingent upon attainment and maintenance of adequate levels of spawning stock biomass by modifying current fishing mortality patterns. Initiating a rebuilding regime whereby recruitment more than replaces the removals from the fishery will insure that the stock begins to recover. With appropriate management the advent of a good year-class could move the stock toward a permanent recovery with realization of past long-term yields in the 35 000 to 50 000 t range.

Acknowledgments

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Temporal and Spatial Trends in Metal Loadings to Sediments of the Turkey Lakes, Ontario

M. G. Johnson, L. R. Culp, and S. E. George

Great Lakes Fisheries Research Branch, Department of Fisheries and Oceans, Owen Sound, Ont. N4K 6H6

Johnson, M. G., L. R. Culp, and S. E. George. 1986. Temporal and spatial trends in metal loadings to sediments of the Turkey Lakes, Ontario. Can. J. Fish. Aquat. Sci. 43: 754–762.

Sediment core profiles of metal concentration and ^{210}Pb activity were used to calculate metal loadings to five small Precambrian Shield lakes of the Turkey Lakes system near Sault Ste. Marie, Ontario. Background, natural concentrations (pre-1900) of Al, Fe, Mn, Cu, Ni, Zn, Pb, Cd, Cr, and Hg reflected concentrations in local bedrock. Surface loading rates of Al, Cu, Ni, and Cr were not significantly greater than background rates. Fe and Mn enrichment of surface sediment and the downstream accumulation in the five lakes indicated the mobility of these elements. Four metals, Pb, Cd, Hg, and Zn, had significant anthropogenic inputs, which averaged 18, 1.7, 1.4, and 0.6 times background loadings, respectively. Precipitation loadings of Pb and Hg were several times greater than background accumulation in lake sediments. Precipitation loadings of Cu, Ni, Zn, and Cd were the same order of magnitude as background inputs to sediments.

On a employé les profils de concentration des métaux, obtenus d'après l'examen de carottes de sédiments, et les profils d'activité du Pb^{210}, pour calculer les charges métalliques reçues par cinq petits lacs du Bouclier précambrien, qui font partie du réseau des lacs Turkey près de Sault Ste. Marie en Ontario. Les concentrations naturelles de fond (avant 1900) d'Al, Fe, Mn, Cu, Ni, Zn, Pb, Cd, Cr et Hg reflétaient les concentrations décelées dans la couche rocheuse locale. Les charges en surface d'Al, Cu, Ni et Cr n'étaient pas nettement plus élevées que les valeurs de fond. L'enrichissement en Fe et Mn des sédiments superficiels et l'accumulation de ceux-ci en aval, dans les cinq lacs, ont indiqué la mobilité de ces éléments. Quatre métaux, Pb, Cd, Hg et Zn, montraient des taux d'introduction anthropogénique significatifs, qui représentaient en moyenne 18, 1,7, 1,4 et 0,6 fois les charges de fond respectivement. Les charges de Pb et Hg dues aux précipitations dépassaient de plusieurs fois les valeurs de fond résultant de l'accumulation de ces éléments dans les sédiments lacustres. Les charges de Cu, Ni, Zn et Cd résultant des précipitations étaient du même ordre de grandeur que les valeurs de fond dues à l'accumulation dans les sédiments.

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Precambrian Shield lakes are receiving increased metal loadings by accelerating atmospheric deposition and possibly by enhanced mobilization of metals attributable to acidification of surface and ground waters. Temporal trends in metal loadings to lake sediments can be estimated from metal concentration profiles in sediment cores and mass sedimentation rates (Kemp and Thomas 1976; Kemp et al. 1978; Nriagu et al. 1979). The method assumes negligible redistribution of metals within the sediment column and relatively uniform mass sedimentation rate through time. The first assumption appears to be valid normally for many metals, including Cu, Ni, Zn, Pb, Cd, Cr, and Hg, but Fe and Mn migrate upward from reducing to oxidizing sites (Mackereth 1966; Kemp and Thomas 1976). The extent of variability in mass sedimentation rate can be assessed by examination of activity profiles of unsupported ^{210}Pb (in secular equilibrium with ^{226}Ra) in relation to cumulative mass with depth in order to substantiate uniform sedimentation (Robbins and Edgington 1975) or to identify periods with different rates (Dominik et al. 1978). Background, or natural, metal loadings are the product of precolonial metal concentrations and the appropriate mass sedimentation rates. Kemp and Thomas (1976) assumed that background concentrations of metals in surface sediments had the same ratio to Al as in precolonial sediment independent of sedimentation rate, which allowed estimation of anthropogenic inputs of metals.

Natural and contemporary metal loading rates were determined in nine cores collected from five lakes of the Turkey Lakes chain located in undisturbed terrain 50 km north of Sault Ste. Marie, Ontario. Natural rates determined from sediment core samples were compared with rates calculated from the elemental composition of bedrock. Anthropogenic loadings, the difference between total surface and estimated background loadings, were compared with precipitation loadings of metals. We measured Al, Fe, Mn, Cu, Ni, Zn, Pb, Cd, Cr, and Hg. As indicated, elevated concentrations of Fe and Mn in surface sediment were not interpreted as anthropogenic inputs. However, because oxygen conditions in summer varied among lakes, we expected to corroborate the migration of Fe and Mn within profiles in response to oxygen gradients.

Inputs to sediments should reflect loadings to lakes through time, which assumes further that the sedimented proportion of lake loadings remains relatively constant. This would require that limnological conditions have not changed markedly, for example, by recent pronounced acidification or altered deoxygenation characteristics, both of which could influence the

TABLE 1. Summary of general morphometric and chemical characteristics of the five study lakes. Data were taken from Jeffries and Semkin (1982) and Jeffries et al. (1983).

Lake	Morphometry			Chemistry			
	Area (ha)	Max depth (m)	Mean depth (m)	pH (median)	Alkalinity ($meq \cdot L^{-1}$)	Ca^{2+} ($meq \cdot L^{-1}$)	Mg^{2+} ($meq \cdot L^{-1}$)
Turkey	52.0	37.0	12.2	6.7	0.190	0.286	0.043
Little Turkey	19.2	13.0	6.0	6.6	0.166	0.259	0.047
Wishart	19.2	4.5	2.2	6.6	0.112	0.200	0.042
Lower Batchawana	5.8	10.9	3.3	6.1	0.070	0.158	0.042
Upper Batchawana	5.9	11.3	3.9	6.0	0.048	0.116	0.037

TABLE 2. Water depth at coring stations, linear and mass sedimentation rates, and % organic matter (mean through each core).

Station	Depth water at station (m)	Sedimentation rate ($mm \cdot yr^{-1}$)	Mass sedimentation rate ($mg \cdot cm^{-2} \cdot yr^{-1}$)	Organic matter (%)
Turkey Main	37.0	0.7	7.0	28
Turkey 1	20.0	0.2	4.5	9
L. Turkey Main	13.0	0.8	5.5	37
L. Turkey 1	7.0	1.3	24.2	24
L. Turkey 2	7.0	0.5	4.5	25
Wishart Main	4.5	1.1	8.3	42
Wishart 1	4.0	1.1	6.2	45
L. Batchawana Main	10.9	1.0	6.9	50
U. Batchawana Main	11.3	0.3	2.0	49

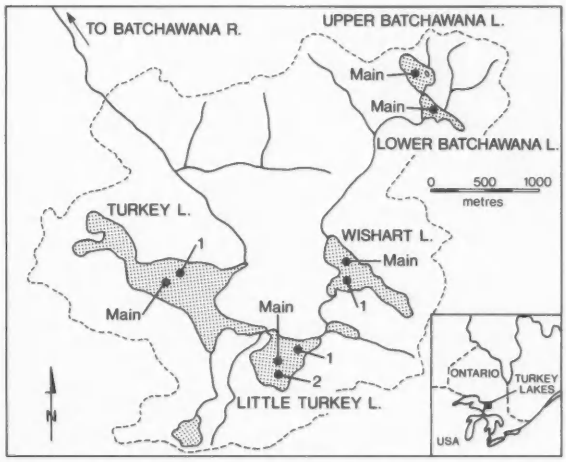

FIG. 1. Station locations in five lakes of the Turkey Lakes system.

mobility of metals. Therefore, recent observations on lake limnology and some paleoecological data were examined in this context.

Study Area

The Turkey Lakes watershed (Fig. 1), 1050 ha in area, is surrounded by mixed forest and is underlain by predominantly intermediate to basic metavolcanic rocks and overlain by basal tills, thinnest at the highest altitudes and thickest in the vicinity of Turkey Lake. The main component of bedrock is tholeiitic basalt which has undergone regional metamorphism (Semkin and Jeffries 1983). Minor occurrences of sulphide mineralization were observed, which may be reflected in lake sediments by elevated background concentrations of Pb, Zn, and Hg.

The two upstream lakes, Upper and Lower Batchawana, are relatively deep considering their small areas (Table 1); they stratify thermally and oxygen depletion in deeper waters begins early and is nearly complete by late summer. They are the most poorly buffered of the five lakes and pH values below 5.0 are typical of surface water during snowmelt. Wishart Lake is polymictic, well oxygenated, and better buffered than the upstream lakes. Little Turkey and Turkey lakes are dimictic, but oxygen depletion is greater in the former (to about 1 $mg \cdot L^{-1}$ over the sediments) than the latter (considerably above 1 $mg \cdot L^{-1}$). Median pH levels are greater in the two downstream lakes. While pH of surface waters of these two lakes has been depressed to pH 5.0 during snowmelt, deeper waters remain between 6.0 to 7.0 at the same time (Jeffries et al. 1983). The two headwater lakes also maintain pH levels near 6.0 in deeper waters during snowmelt episodes. In the lakes where oxygen depletion occurs in hypolimnetic waters, pH depression (H^+ contributed by heterotrophic processes) in late summer is slightly greater than in water at comparable depth during the spring freshet. Our data on chironomid and chaoborid remains in cores suggest relatively uniform conditions at least with respect to oxygen and pH regimes through the past few hundred years.

Methods

Sediment cores were collected in 1981 and 1982 from nine stations (Fig. 1; Table 2), five of which were from the main stations at approximately maximum depth in each lake. Three cores were obtained at each site utilizing a KB corer modified

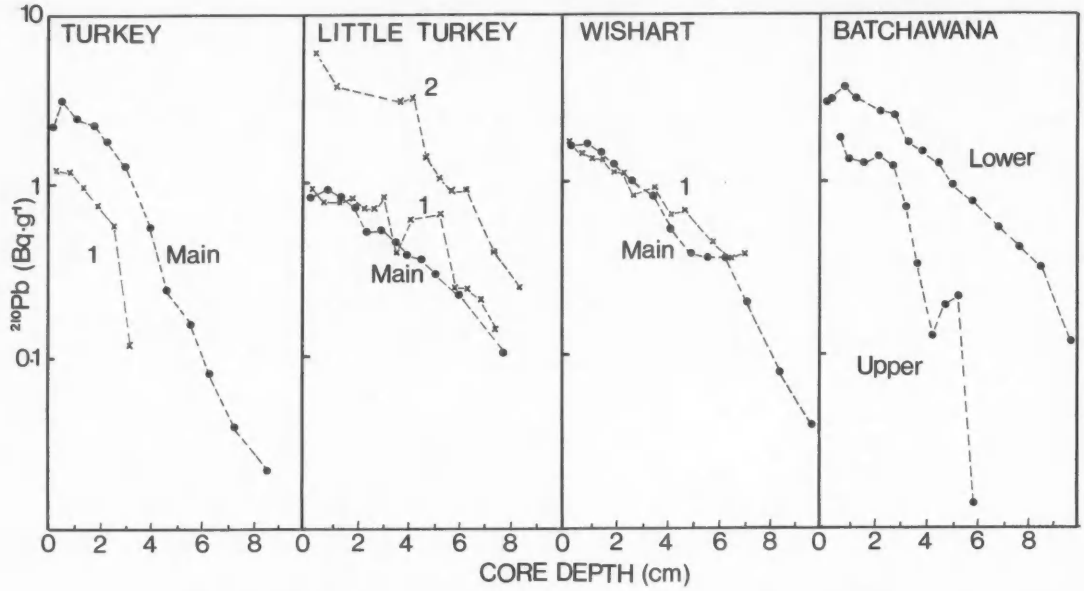

FIG. 2. Activity of ^{210}Pb (based on dried sediment weight) with depth in the nine cores.

to accept Benthos corer tubes of 6.6-cm diameter. Two cores were split at 1-cm intervals to 10 cm and at 2-cm intervals to 20 cm. Our core extruder discarded the outer 0.8 cm to eliminate effects of smearing along the core tube surface. Sediment was freeze-dried and analysed for percent moisture, particle size by techniques of Rukavina and Duncan (1970), loss on ignition (as an estimator of organic matter), and metals. A third core was sectioned and analysed for ^{210}Pb by Drs. R. W. Durham and S. R. Joshi at the National Water Research Institute, Burlington, Ontario. Their methods are described elsewhere (Durham and Joshi 1984).

Metals analysis was contracted to Barringer Magenta Ltd., Toronto, Ontario. Freeze-dried sediment was digested in nitric, perchloric, and hydrofluoric acids to remove organic and silicate material. The digest was then dried, resuspended with 0.5 *M* HCl, and analysed for Al, Fe, Mn, Cu, Ni, Zn, and Cr by inductively coupled plasma emission spectrophotometry. Because of interference by other elements, Cd and Pb were determined on a Varion AA-5 atomic absorption spectrophotometer. Mercury was determined utilizing cold vapor atomic absorption. Detection limits for trace elements were as follows: Cu, 0.3 $\mu g \cdot g^{-1}$; Ni and Zn, 2.0 $\mu g \cdot g^{-1}$; Pb, 5.0 $\mu g \cdot g^{-1}$ on 1981 samples and 2.0 $\mu g \cdot g^{-1}$ on 1982 samples; Cd, 0.8 $\mu g \cdot g^{-1}$ on 1981 samples and 0.2 $\mu g \cdot g^{-1}$ on 1982 samples; Cr, 0.8 $\mu g \cdot g^{-1}$; Hg, 4.0 $ng \cdot g^{-1}$. At least 10% of the samples were replicated and standard reference sediments were submitted at random among other samples. Cu, Ni, Zn, and Pb concentrations were within 10% of the reference concentrations. Hg was within 20% and Cd was within 40%. Detection levels were generally adequate for this study but greater precision for Hg and Cd would have been desirable.

Results

Sedimentation Rates

Mass sedimentation rates (Table 2) varied from 2.0 to 24.2 $mg \cdot cm^{-2} \cdot yr^{-1}$ at the Upper Batchawana and Little Turkey 1 stations, respectively. The other seven stations had rates of 4.5–8.3 $mg \cdot cm^{-2} \cdot yr^{-1}$. The mean rate was 7.7 $mg \cdot cm^{-2} \cdot yr^{-1}$. Standard deviations of individual estimates were <30% and the average was 15.5% (Durham and Joshi 1984). Linear sedimentation rates averaged 0.8 $mm \cdot yr^{-1}$ and their standard deviations averaged 11.2%. Sedimentation was uniform through time. Activity of ^{210}Pb with depth (Fig. 2) indicated some mixing, probably only to about 1 cm or less at most stations. Exceptional cores were Upper Batchawana (partially mixed to 2 cm) and Little Turkey 1 and 2 (partially mixed to 3 cm). The bias introduced by mixing in interpretation of metal concentration profiles and anthropogenic loading rates will be discussed subsequently.

With the exception of Turkey Lake station 1, sediments had organic matter content of 24–50%, with the highest values in the two upper lakes, 50 and 49%, and a decline downstream in the lake chain (Table 2). This decline may be the result of increased lake size, with reduction of shoreline length to area ratio, as well as interception of detritus by upstream lakes. The low organic matter (9%) in the shallower station in Big Turkey Lake was not expected at 20 m depth, indicating currents at significant depth in larger lakes. Sedimentation in terms of inorganic material (corrected for organic matter) varied from 1.0 to 18.4 $mg \cdot cm^{-2} \cdot yr^{-1}$.

Interpretation of Concentration Profiles

General observations

Some general patterns in metal concentration profiles (Fig. 3) will be described here and subsequently examined in more detail. First, some metals showed trends among lakes. Al, Fe, and Mn concentrations increased downstream from Upper Batchawana to Turkey Lake, especially Mn with close to one order of magnitude range in concentration. The possibility of dilution in upstream lakes by organic matter will be examined. Cu at main stations also showed a downstream

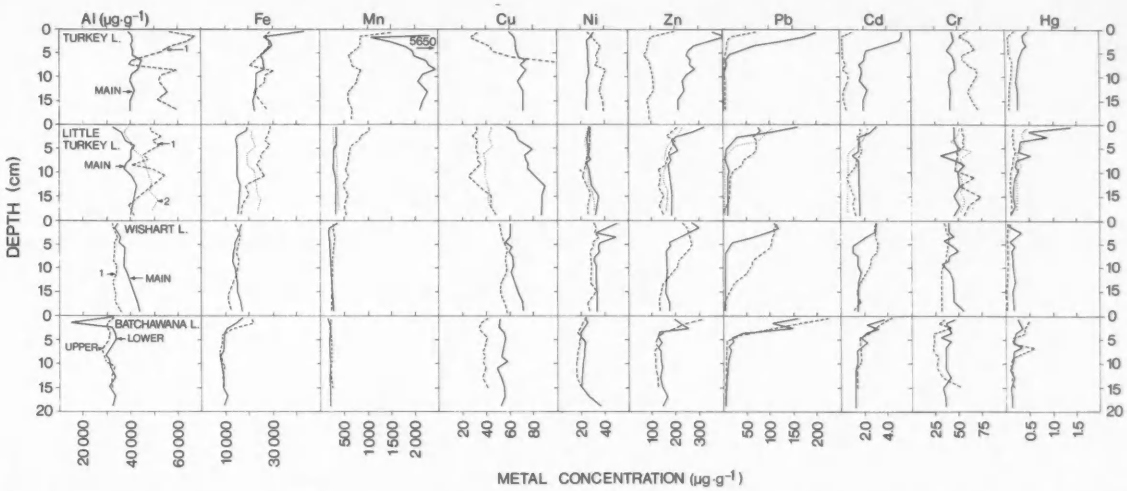

FIG. 3. Concentration profiles of 10 metals in the nine cores. The vertical location of the year 1900 is shown for each core on the Al concentration profile.

increase in concentration. However, the differences in Cu concentrations between main stations and shallower stations suggest a stronger relationship with depth than with organic matter (see Fig. 3). In contrast, concentrations of other metals were relatively uniform from lake to lake and their vertical profiles were similar in most cases.

Vertical profiles showed consistently elevated concentrations of Pb, Zn, and Cd in recent sediments (Fig. 3). Two atypical features of these 27 profiles were, first, the lower concentrations in the core Turkey 1 and the more gradual, almost linear, rise in concentration in Wishart 1 core. The Turkey 1 core had the coarsest texture of all cores. Consequently, while the profile had the mid-depth inflection of the others, the lower concentrations indicated dilution by coarser sediment particles. The Wishart 1 core demonstrated the effect of moderate sediment mixing, which tended to blur the profile in contrast with the sharper inflections in profiles in the deeper cores from dimictic lakes. Vertical profiles of Hg usually showed enrichment in near-surface sediment. Hoewever, Hg profiles exhibited more variability than Pb, Zn, and Cd which appears likely to be attributable to greater analytical error with Hg. Ni, Cr, and usually Cu had relatively constant profiles. Ni and Cr, unlike Cu, showed little difference among profiles within lakes.

Background concentrations

Metal concentration profiles were examined for points of inflection in relation to cumulative age of sediment sections. Background (natural) concentrations occurred most often in sections that were 100 yr old and deeper. Points of inflection were defined as the first core slice that exceeded the mean background concentration plus two standard deviations. Mean background concentrations at each station were calculated in two forms, the first based on total sediment weight and the second on inorganic weight (Table 3). The latter were compared with concentrations of metals (except Cd) in bedrock collected in the watershed (Semkin and Jeffries 1983). There was no statistical difference between mean concentrations in cores (based on inorganic fraction) and in bedrock samples for Al, Cu, and Pb. Mean concentrations in cores were greater than in bedrock for Zn (2 times) and Hg (5 times) and less than in bedrock for Fe (4 times), Mn (2 times), Ni (2 times), and Cr (2 times).

Variability in metal concentrations among cores was expected to be least for ubiquitous elements and greatest for less abundant and irregularly distributed elements. This was true for Al and Fe which had low variances (evident in low standard errors relative to means in Table 3) in bedrock and core concentrations and for Pb and Hg (two of the three least abundant metals with Cd) with high variances. Variability was intermediate in Cu, Ni, and Zn and it was considerably less in pre-1900 lake sediments than in bedrock. Variances of these metals in lake sediments were reduced to levels nearer variances in Al and Fe, indicating a smoothing effect through weathering and subsequent deposition. This occurred also in the case of Pb and Hg but to a lesser extent. Considerably higher variability of Mn in lake sediments relative to bedrock was unexpected but this was caused mainly by the increase in Mn concentrations from upstream to downstream lakes.

Pre-1900 concentrations may be subtracted from surface values to estimate anthropogenic contributions to concentrations and ultimately to partition surface loading rates into background and anthropogenic components. This assumes no temporal change in background concentration at a given station which might occur, for example, if organic and inorganic fractions changed or mass sedimentation rate varied from pre-1900 to present times. We concluded that sedimentation was uniform through time. Therefore, we examined variability in background concentrations of metals in core slices within each lake in relation to organic matter and Al concentrations. The majority of correlation coefficients was insignificant with each independent variable. The minority of significant coefficients was negative or positive with little relationship to either metal or lake. The only strong relationship was a negative one between the two independent variables, organic matter and Al. Because of these results and the high probability of relatively uniform mass sedimentation rates there was no justification for correction of pre-1900 concentration to be used to partition surface loading rates into background and anthropogenic, such as the Al "normalization" procedure used by Kemp and Thomas

TABLE 3. Background metal concentrations in cores and mean concentrations for nine stations (shown in Fig. 1) based on total weight. A second set of mean background concentrations is based on inorganic weight (corrected for organic matter). Mean concentrations of metals in local bedrock are from Semkin and Jeffries (1983). Asterisks indicate means significantly different from mean concentrations in bedrock ($p = 0.05$).

	$mg \cdot g^{-1}$			$\mu g \cdot g^{-1}$						
Station	Al	Fe	Mn	Cu	Ni	Zn	Pb	Cd	Cr	Hg
Turkey Main	41.7	24.1	2.23	71.9	27.0	246.9	4.3	1.9	43.1	0.24
Turkey 1	55.5	27.3	0.76	46.3	35.3	81.8	7.5	0.2	61.8	0.04
L. Turkey Main	40.0	15.5	0.32	82.9	30.0	179.0	6.9	1.5	48.8	0.18
L. Turkey 1	42.9	17.8	0.54	43.2	26.5	140.8	5.3	1.1	59.0	0.10
L. Turkey 2	46.9	21.6	0.37	40.6	28.4	159.2	5.6	0.6	54.2	0.15
Wishart Main	41.9	15.7	0.26	68.6	33.5	169.3	5.0	1.5	47.5	0.15
Wishart 1	34.1	12.3	0.23	55.0	29.2	141.0	9.6	1.5	32.7	0.23
L. Batchawana Main	31.7	8.8	0.18	52.6	23.8	140.5	6.7	1.1	35.5	0.13
U. Batchawana Main	29.8	8.3	0.20	37.5	16.8	113.9	9.1	1.3	28.9	0.24
Mean total wt.	40.5*	16.8*	0.57*	55.4	27.8*	152.4	6.7	1.2	45.7*	0.16
Standard error	2.5	2.1	0.22	5.3	1.8	15.3	0.6	0.2	3.9	0.02
Mean inorganic wt.	62.0	24.8*	0.81*	87.9	43.2*	241.2*	7.8	2.0	69.5*	0.27*
Standard error	1.6	1.9	0.29	9.9	2.9	24.8	1.5	0.3	3.1	0.04
Mean bedrock	75.8	95.4	1.64	75.3	81.3	115.6	17.6	<2	165.3	0.05
Standard error	3.7	6.3	0.11	14.5	14.2	13.2	6.7	—	42.0	0.04

TABLE 4. Metal concentrations at 0−1 cm in cores, and average ratios of these surface concentrations to background concentrations. Core stations are shown in Fig. 1 Asterisks indicate surface to background (S:B) ratios significantly different from 1.0 ($p = 0.05$).

	$mg \cdot g^{-1}$			$\mu g \cdot g^{-1}$						
Station	Al	Fe	Mn	Cu	Ni	Zn	Pb	Cd	Cr	Hg
Turkey Main	38.8	43.8	5.65	60.8	26	355	200	5.2	43.8	0.45
Turkey 1	56.3	28.6	1.54	33.1	32	187	72	1.0	60.2	0.15
L. Turkey Main	32.5	19.6	0.36	58.9	27	325	155	3.0	45.0	1.34
L. Turkey 1	49.5	29.2	1.03	31.7	29	213	74	1.6	53.5	0.16
L. Turkey 2	38.6	19.3	0.31	44.8	28	227	106	2.2	52.5	0.44
Wishart Main	34.3	17.2	0.36	61.4	51	272	110	3.0	40.0	0.10
Wishart 1	32.1	13.7	0.30	51.2	31	235	116	3.1	34.9	0.50
L. Batchawana Main	31.0	16.2	0.14	50.8	23	187	155	3.5	45.0	0.26
U. Batchawana Main	32.1	20.4	0.21	40.1	23	309	220	4.0	33.8	0.48
Mean surface	38.4	23.1	1.10	48.1	30	257	134	3.0	45.4	0.43
Standard error	3.0	3.1	0.59	3.8	2.8	20.5	17.4	0.42	2.9	0.13
Mean S:B ratio	0.95	1.46*	1.48*	0.90	1.09	1.76*	21.4*	2.81*	1.01	2.72*
Standard error	0.04	0.17	0.20	0.05	0.07	0.15	3.6	0.36	0.04	0.66

(1976) and Kemp et al. (1978). Also, profiles of organic matter and Al were considerbly more uniform than most of the other metals.

Surface concentrations

Concentrations of metals at 0−1 cm (Table 4) relative to background concentrations were usually significantly different for Fe, Mn, Zn, Pb, Cd, and Hg, and not different, on average, in the cases of Al, Cu, Ni, and Cr. A minority of Al and Cu profiles showed decreases in concentration toward the surface.

Elevated concentrations of Fe and Mn at 0−1 cm relative to pre-1900 levels occurred in some cores, and the mean of the ratio of surface to background concentrations was significantly greater than 1.0 in both cases (Table 4). Fe concentrations were significantly elevated (that is, greater than two standard deviations above mean background values) in cores at all main stations, except in Wishart Lake. They were not elevated at shallower stations. The pattern for Mn was different in part, with no elevated concentrations in Upper Batchawana, Lower Batchawana, and the main station in Little Turkey Lake and elevated concentrations in most other cores. The pattern for Mn showed the expected surface accumulations in oxygenated systems and linear profiles in deoxygenated systems (Kemp and Thomas 1976). Furthermore, the low Mn concentrations in sediments of Upper and Lower Batchawana, approximately 200 $\mu g \cdot g^{-1}$, and considerably higher concentrations in downstream lakes, especially Turkey Lake, about 600 $\mu g \cdot g^{-1}$, suggest mobility on a larger scale. The downstream increase occurred in both surface and the deepest, background sediments, which indicates that the process is unrelated to anthropogenic factors. Although Fe concentration profiles did not parallel Mn profiles in every core, Fe also showed this downstream increase in concentration from <9000 $\mu g \cdot g^{-1}$ in Upper and Lower Batchawana to >20 000 $\mu g \cdot g^{-1}$ in Turkey Lake. Fe also increased downstream as much in background sediments as in surface sediments. The downstream increase in Fe and Mn

in sediments indicates the possibility of unloading of these metals from sediments to water, and from lake to lake. Surface enrichment of sediments by Fe and Mn likely was due to upward migration, as observed by Kemp and Thomas (1976).

Surface concentrations of Zn, Pb, Cd, and Hg were significantly different than background within every core except one metal in one core (Hg in Wishart Lake Main core). In this core the 0–1 cm concentration was depressed and it was not significantly different from background. Two deeper core slices had significantly higher concentrations. We cannot account for this anomaly.

The calculated maximum ages within each core where metal concentrations were significantly different from background were calculated. The Turkey 1 core was excluded because each core slice represented considerably more time than in other areas (2 cm was equated to 169 yr). These inflection points occurred on average at 74–83 yr before sampling, that is, about 1900–10. The confidence intervals, 20–25 yr, were particularly broad because of low mass sedimentation rates in relation to thickness of core slices. Also, variability in background concentrations and some in situ mixing impair identification of actual inflection points. In one case, the Wishart Lake Main station, inflection points were much later compared with other cores, 36 yr before sampling for Zn and Pb and only 25 yr for Cd and Hg. The ^{210}Pb profile for that core indicated constant sediment accumulation with time (Fig. 2) but the possibility exists of loss of top sediment at some time.

Rates of change in concentration of Zn, Pb, Cd, and Hg were determined in regressions of concentrations versus age using core slices down to the inflection point plus one adjacent background slice. These rates (micrograms per gram per year) averaged 1.6 for Zn and Pb, 0.027 for Cd, and 0.0023 for Hg. The percentage rates of increase (calculated over 80 yr) corresponding to the surface to background ratios in Table 4 are 0.8% for Zn, 3.9% for Pb, and 1.3% for both Cd and Hg.

There were three cores that had significantly higher Ni in surface slices compared with background. Two of these were borderline with a single sample slightly greater than the upper confidence limit on background concentration. The third from the Wishart Lake Main station had enrichment typical of Zn profiles. Based on this limited evidence, we cannot conclude that anthropogenic enrichment of Turkey Lake sediments by Ni has occurred yet.

The central question on Cu profiles was the significance of apparent declines toward the surface. While six cores showed no significant decrease in concentration near the surface, one core (Turkey 1) had a prominent decrease and two cores (Turkey Main and Little Turkey Main) had small but significant declines in concentration nearer the surface. Because of the possibility of dilution of Cu with organic matter, we repeated calculations using concentrations based on the inorganic fraction. The declines remained significant. Although these "inverse profiles" of Cu occurred in a minority of cores, the data suggest a decline in loadings or redistribution in sediments or loss to the water after deposition at these sites.

Profiles of Al were usually linear, but three cores had "inverse profiles" (Little Turkey Main and 2 and Wishart Main). Correlation between Al and organic matter was high; therefore, Al values adjusted for organic matter were much closer to background concentrations. Some Al concentrations remained significantly less than background. However, because these differences were relatively low, occurred in only three cores, and were explained to a considerable extent by dilution by the organic fraction, we view Al inputs to these sediments as generally constant with time. The same conclusion was made readily for Cr.

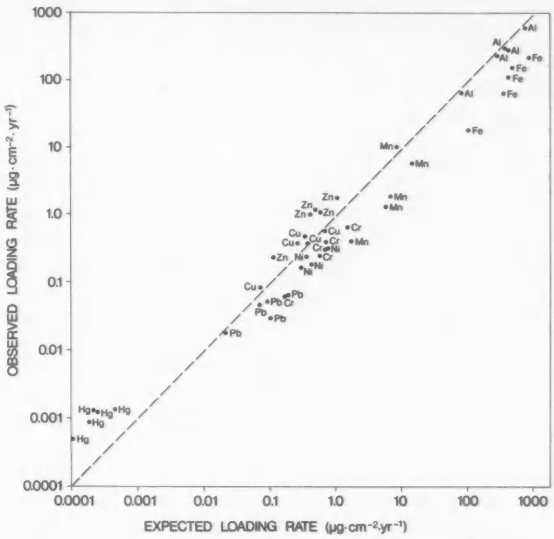

FIG. 4. Observed background loading rates of 10 metals (averaged for each lake) compared with expected loading rates calculated from concentrations in bedrock samples collected in the Turkey Lakes watershed by Semkin and Jeffries (1983) and sedimentation rates of the inorganic fraction.

Loading rates

Natural loading rates of metals determined from core concentrations and averaged for each lake were compared with loading rates calculated from data on elemental concentrations in bedrock and inorganic fractions of the mass sedimentation rates (Fig. 4). Differences described previously for each metal in terms of concentrations are apparent. However, the overall relationship, considering all metals, shows that natural loading rates of metals to lake sediments are generally of the same order of magnitude as those predicted by their elemental composition in bedrock and sedimentation rates of inorganic material.

The high variability in mass sedimentation rates (one order of magnitude) contributed to high variability in metal loading rates (Table 5). Surface and background loading rates of Al were similar. Because of the upward mobility of Fe and Mn, and loss to the water phase suggested by the downstream gradient in concentrations, their actual net loading rates probably would be close to the background loading rates. Surface loading rates of Cu were within 20%, for Ni within 9%, and for Cr within 3% of background rates. Based on statistical interpretation of concentration profiles, anthropogenic inputs of Cu, Ni, and Cr were not detectable. Four metals had significant anthropogenic inputs (Fig. 5). Anthropogenic inputs were 0.6 times background for Zn, 18 times for Pb, 1.7 times for Cd, and 1.4 times for Hg.

Atmospheric (precipitation) loadings were obtained from Ontario Ministry of the Environment (1983) deposition maps based on data from Sangamo collectors operated at 36 sites. Annual deposition rates for 1981 of Al, Fe, Mn, Cu, Zn, Pb, and Cd were obtained. The deposition rate of Ni was obtained from Kramer (1976) and Jeffries (1975), included in the review

TABLE 5. Mean loading rates for 10 metals. Surface loading rates were calculated from concentrations at 0–1 cm in cores. Background loading rates were based on pre-1900 concentrations. Anthropogenic loading rates are means of the differences. Precipitation loadings are values from the literature converted to $\mu g \cdot cm^{-2} \cdot yr^{-1}$. ND = not detected.

Loading rate ($\mu g \cdot cm^{-2} \cdot yr^{-1}$)	Al	Fe	Mn	Cu	Ni	Zn	Pb	Cd	Cr	Hg
Surface mean	315	121	9.0	0.35	0.24	1.88	0.887	0.020	0.37	0.003
Standard error	112	25	4.6	0.07	0.07	0.46	0.159	0.004	0.12	0.0007
Background mean	317	132	4.5	0.42	0.21	1.19	0.047	0.009	0.38	0.001
Standard error	94	40	1.9	0.10	0.06	0.32	0.011	0.0026	0.13	0.0002
Anthropogenic mean	ND	ND	ND	ND	ND	0.69	0.840	0.015	ND	0.002
Standard error	—	—	—	—	—	0.15	0.151	0.004	—	0.0006
Precipitation	6.5	5.5	0.3	0.3	0.4	0.8	0.4	0.01	0.03	0.003–0.006

by Jeffries and Snyder (1981). Kramer (1976) provided an estimate for Cr. Information on concentrations of Hg in precipitation and loading rates is scarce, but we have unpublished data from 59 event samples taken in 1980–81 near Tobermory, Ontario (Table 5).

Precipitation loadings of Al, Fe, Mn, and Cr were minor (2–8%) relative to background loadings and therefore could not be detected in sediment cores (even if they were anthropogenic). Precipitation loadings of Cu, Ni, Zn, Cd, and Hg were approximately the same magnitude as background loadings, but we found significant anthropogenic inputs for Zn, Cd, and Hg only. Precipitation loadings of Cu and Ni usually are not reflected by anthropogenic peaks in these sediments. In contrast, precipitation loadings of Pb were close to one order of magnitude greater than background loadings and Pb had the highest ratio (18 times) of anthropogenic to background inputs. This comparison of anthropogenic loadings with direct precipitation loadings suggests a high degree of retention of Pb in lakes, which may be because Pb in precipitation is largely organolead with large potential for biological uptake.

Discussion

Background loadings of metals to these lakes generally reflected the elemental composition of local bedrock. Reduced variability in metals of lesser abundance in lake sediments relative to bedrock indicated the integrating effect of weathering and sedimentation. Greater concentrations of Zn and Hg in lake sediments than in bedrock suggested occurrence of minerals in the watershed (sphalerite perhaps) not well represented in bedrock samples, a possibility raised by Semkin and Jeffries (1983). Fe and Mn were less abundant in pre-1900 lake sediments than in bedrock but our data indicated the upward mobility of Fe and Mn in sediments and downstream translocation. Comparison of the concentration of remaining Fe, based on the inorganic fraction of sediment, with concentration in bedrock (Table 3) indicated that only 18–35% of Fe was retained in net deposition. Results were similar for Mn in the upper four lakes, 23–26% retained, but Turkey Lake may have held most of its Mn loading. Ni and Cr also were less abundant in lake sediments than in bedrock, but there was no evidence of mobility in lake sediments or losses downstream through the system. Mean concentrations of Al, Cu, and Pb were not significantly different between bedrock and pre-1900 lake sediment. Found Lake, Ontario (Evans and Dillon 1982), and Mountain Pond, Maine (Hanson and Norton 1982), had background loading rates of Pb very close to the rate of 0.05 $\mu g \cdot cm^{-2} \cdot yr^{-1}$ measured in the Turkey Lakes. Background loadings of Cu, Zn, Cd, and Hg in Georgian Bay sediments were within 30% of Turkey Lakes study area loadings, but background loadings of Ni, Cr, and Pb were 3 times greater in Georgian Bay (M. G. Johnson, unpubl. data).

Surface loading rates of Al, Cu, Ni, and Cr were not significantly greater than background rates in the Turkey Lakes. This was expected for Al and Cr because of extremely low precipitation loadings relative to background loadings to sediments. Both Ni and Cu showed precipitation inputs of similar magnitude to background loading rates in sediments, and therefore, detectable anthropogenic loadings were expected. One core only (Wishart Main) had a near-surface increase in the concentration of Ni. However, the accuracy of precipitation loadings, data, and the magnitude of natural precipitation loadings of Cu and Ni remain uncertain.

Cu enrichment in surface sediments is typical throughout the Great Lakes, in some lakes near Sudbury, Ontario (Crocket and Kabir 1981), in New England lakes where precipitation inputs of Cu are several times greater than in northern Ontario (Galloway and Likens 1979), but not in northern Wisconsin lakes (Iskandar and Keeney 1974). Enrichment of surface sediments by Ni was observed in Lake Huron and Georgian Bay (M. G. Johnson, unpubl. data) and near Sudbury (Crocket and Kabir 1981), probably both related to Ni smelting at Sudbury, Ontario. Enrichment in Ni was not obvious in the northern Wisconsin lakes or in Lake Superior. This evidence suggests that Cu and Ni atmospheric inputs have not changed sufficiently in northern areas, relative to their background loadings and their specific limnological behavior, to create detectable enrichment profiles. Where enrichment occurs in northern areas it has been attributed to mining activities, such as Ni in Georgian Bay and Cu in Lake Superior. At three sites, Cu concentrations decreased near the surface, which suggested either reduction in input or the possibility of unloading from the sediments. Input reduction is unlikely. Unloading from sediments also appears unlikely because the stations exhibiting "inverse profiles" were in Turkey and Little Turkey lakes where oxygen and pH were higher (than in Upper and Lower Batchawana, for example). However, inverse profiles or subsurface peaks may result from downward "biodiffusional transport" (Carignan and Tessier 1985).

Surface sediment enrichment by Fe and Mn occurred in the majority of cores; because of the evidence for translocation, the known kinetics of Fe and Mn in sediments, and extremely low precipitation loadings relative to background loadings to sediments, this does not indicate anthropogenic loadings.

The three metals Zn, Pb, and Cd consistently showed enrichment in the Turkey Lakes, throughout the Great Lakes, and in

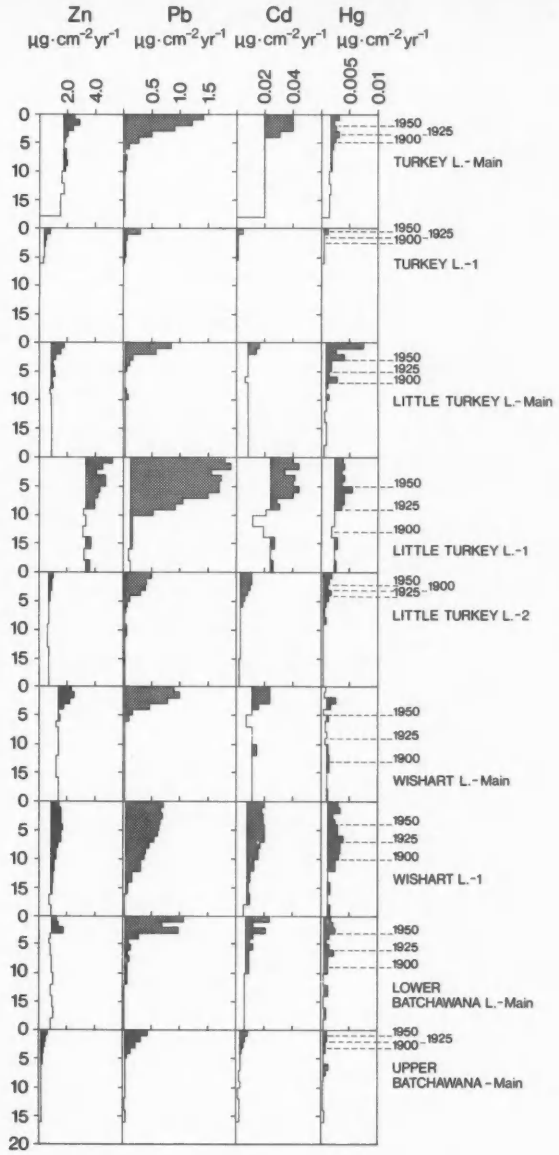

FIG. 5. Loading rates to each of nine stations in the Turkey Lakes system for Zn, Pb, Cd, and Hg. Shaded areas show calculated anthropogenic inputs.

lakes of northern Wisconsin, New York, and New England. Less data are available on Hg, perhaps because of analytical difficulties, but enrichment is usually observed in the Great Lakes. The age of sediments at the point of earliest anthropogenic inputs of Pb, Zn, Cd, and Hg usually corresponds to the period 1875–1900; onset of enrichment appears to be earlier in the lower Great Lakes region than in the upper Great Lakes region (Kemp and Thomas 1976). The degree of enrichment is generally Pb ≫ Cd > Hg > Zn. Pb is outstanding with surface inputs 18 times background in this study, at least 25 times in Found Lake, Ontario (Evans and Dillon 1982), 10 and 150 times in two Adirondack lakes, 4.3 times in one New Hampshire lake (Galloway and Likens 1979), and 4–9 times in main basins throughout the Great Lakes.

The degree of enrichment (indicated by surface to background concentration ratios) and calculated present loading rates would be affected by vertical mixing within sediments. Profiles of Pb activity indicated mixing to approximately 1 cm deep in the majority of cores, but mixing to 2–3 cm probably occurred in three cores (Fig. 2). Hypothetical calculations were made to examine this issue. We obtained simulated concentration profiles of two metals, one with an increase in input of 1% per year over 80 yr and showing a surface to background ratio of about 2:1 (like Zn, Cd, Hg) with no vertical mixing, and the other which increased 4% per year to produce a ratio of approximately 25:1 (like Pb). The sediment accumulation rate was 1 mm·yr^{-1}, complete mixing to 2 and 3 cm was simulated, and the relative underestimation of concentration in surface sediment was determined for each metal and mixing depth. Underestimates of 5 and 14% occurred in concentration of the first metal with 2- and 3-cm mixing, respectively. Parallel results were 25 and 47% for the second metal. We concluded that surface concentrations of metals with low rates of increase (Zn, Cd, Hg) were not seriously underestimated, but the error could be considerable in the case of Pb. Nonetheless, evidence for high anthropogenic loading of Pb remains valid, and in fact, estimates of the anthropogenic inputs compared with natural inputs are conservative. Bias in loading rates may be expected in any study based on relatively few cores because of spatial variability (Dillon and Evans 1982; Evans and Dillon 1982). Our core stations were deeper than average depths of the Turkey Lakes; therefore, mass sedimentation rates and metal loading rates probably were overestimated. Good agreement between precipitation loadings and anthropogenic loadings (Table 5) may have occurred in part because underestimation due to mixing was offset more or less by overestimation attributable to station selection.

Spatial trends within the Turkey Lakes system were identified only for Fe and Mn. Comparisons of metals concentrations in bedrock and among sediments in the five lakes indicated the downstream translocation of Fe and Mn. There are no physiographic features (swamps, bogs) which might account for increased Fe and Mn loadings downstream through the Turkey Lakes chain. There was no evidence of similar downstream mobility with other metals. Higher concentrations of metals which occurred in the lower lakes were accounted for by less dilution with organic matter.

Unloading of metals from acidified lakes has been reported; for example, Hanson and Norton (1982) reported leaching of Zn from lake sediment during progressive acidification of lakes. The "inverse profiles" of Zn which they observed were not observed in the Turkey Lakes, where water in contact with all but the shallowest sediments had pH between 6.0 and 7.0. However, in three of nine Cu profiles, concentrations decreased toward the surface. Recent evidence (Carignan and Tessier 1985) supports redistribution of Zn within the sediment column rather than unloading. Redistribution seems more likely than unloading of Cu from these three cores because they were from the two downstream lakes least affected by acid loadings.

In summary, relatively uniform profiles of Al, Ni, and Cr in all lakes indicate that loadings of these metals to lake sediments have not increased through time. Some cores suggest in situ redistribution of Cu. Surface enrichment by Fe and Mn

is not by anthropogenic loadings but by vertical diffusion to the water column. Downstream translocation of Fe and Mn appeared to be substantial. Anthropogenic loadings of Zn, Pb, Cd, and Hg were shown by all cores and they were the same order of magnitude as and probably the result of precipitation inputs, a conclusion that is consistent with many other studies (Kemp and Thomas 1976; Kemp et al. 1978; Galloway and Likens 1979; Christensen and Chien 1981; Crocket and Kabir 1981; Evans and Dillon 1982; Hanson and Norton 1982). Also, these data on lake sediments provide evidence that precipitation loadings of Zn, Pb, Cd, and Hg are largely anthropogenic.

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Effect of Body Form and Response Threshold on the Vulnerability of Four Species of Teleost Prey Attacked by Largemouth Bass (*Micropterus salmoides*)

P. W. Webb

School of Natural Resources, University of Michigan, Ann Arbor, MI 48109-1115, USA

Webb, P. W. 1986. Effect of body form and response threshold on the vulnerability of four species of teleost prey attacked by largemouth bass (*Micropterus salmoides*). Can. J. Fish. Aquat. Sci. 43: 763–771.

Experiments were performed using four prey species (fathead minnow, *Pimephales promelas*, largemouth bass, *Micropterus salmoides*, bluegill, *Lepomis macrochirus*, and tiger musky, *Esox* sp.) with various body and fin forms attacked by largemouth bass predators to determine how body and fin morphology, performance, and response thresholds influenced prey vulnerability. Prey differed in three factors that could affect the outcome of predator–prey interactions: body depth, the presence of spiny rays, and locomotor performance capability. Captures were only successful for strikes near the center of mass. The presence of spines was not shown to substantially affect predator strike targets on prey, but large body depth misdirected strikes from the center of mass area and increased the probability of prey escaping. Prey escape speeds were variable and not maximum. Acceleration rates in the startle response varied among the prey species. Tiger musky had the highest acceleration rates (11.7–12.2 $m \cdot s^{-2}$). Acceleration rates decreased for the other prey in the order bluegill, largemouth bass, and fathead minnow. Predators attacking prey with higher acceleration performance were more likely to abort attacks and less likely to chase prey. Prey response thresholds were defined as the rate of change of the angle subtended by the predator as viewed by the prey at the start of the prey's motor response. This looming threshold varied among the species tested, and predators were more likely to abort attacks on prey with low thresholds. Low prey response thresholds correlated with high acceleration rates. The basis for multiple, rather than complementing, adaptations facilitating prey escape is not known, but may be related to risks and benefits during foraging by fish with different diets.

On a réalisé des expériences avec des proies de quatre espèces (tête-de-boule, *Pimephales promelas*, achigan à grande bouche, *Micropterus salmoides*, crapet arlequin, *Lepomis macrochirus* et maskinongé, *Esox* sp.) dont le corps et les nageoires avaient des formes diverses et ayant comme prédateur commun l'achigan à grande bouche. Ces expériences visaient à déterminer comment certaines caractéristiques des proies, comme la morphologie du corps et des nageoires, la performance natatoire et les seuils de réaction influent sur leur vulnérabilité. Les proies se différenciaient par trois facteurs pouvant influer sur l'issue des interactions prédateurs–proies : la hauteur du corps, la présence de rayons épineux et la capacité locomotrice. La capture des proies ne réussissait que si le prédateur frappait près du centre de masse. La présence d'épines ne semblait pas avoir d'effet substantiel sur la partie visée par les prédateurs, mais lorsque la hauteur du corps était grande, les prédateurs avaient du mal à diriger leur attaque près du centre de masse, accroissant les chances de fuite de la proie. Les vitesses des proies en fuite étaient variables et non maximales. Les taux d'accélération après la réaction d'alarme variaient d'une espèce à l'autre. Le maskinongé avait le taux d'accélération le plus élevé (11,7 à 12,2 $m \cdot s^{-2}$). L'accélération allait en décroissant chez le crapet arlequin, l'achigan à grande bouche et le tête-de-boule. Les prédateurs qui attaquaient des proies ayant une accélération plus grande étaient plus susceptibles d'interrompre leur attaque et moins susceptibles de poursuivre leur proie. Les seuils de réaction des proies ont été définis comme étant le taux de changement de l'angle sous-tendu par le prédateur tel que vu par la proie au début de la réaction motrice de celle-ci. Ce seuil d'esquive variait parmi les espèces testées, les prédateurs étant plus susceptibles de renoncer à attaquer les proies ayant un seuil peu élevé. Les seuils peu élevés de réaction des proies ont été corrélés avec des taux élevés d'accélération. On ne connaît pas les raisons régissant les adaptations multiples plutôt que complémentaires qui facilitent la fuite des proies, mais il pourrait y avoir un lien avec les risques et les avantages des différents types d'alimentation des poissons.

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The outcome of a predator–prey interaction depends on the behavior of the participants, which is expected to be influenced by their physical capabilities. Relationships among body and fin form, swimming speed, acceleration, maneuverability, and the outcome of interactions are not well known, and experimental studies are rare. Observations on fish have shown that body and fin form influence the strike behavior of piscivores, but surprisingly, locomotor performance levels are often lower than maximum capabilities (Nyberg 1971; Webb 1984a). Therefore, the role of form in predator behavior is one of permitting but not limiting behavior. This situation may be different for prey because unsuccessful prey do not have second chances.

Body and fin form and locomotor performance can improve prey success in escaping predator attacks in three ways: (1) misdirect attacks from optimal targets on the prey body; (2) im-

TABLE 1. Summary of morphometrics of the prey species. The derivation of the acceleration coefficient is described in the text.

	Fathead minnow (*Pimephales promelas*)	Largemouth bass (*Micropterus salmoides*)	Bluegill (*Lepomis macrochirus*)	Tiger musky (*Esox*)
Total length, L (cm)	5.8±0.2	5.1±0.1	6.4±0.3	6.5±0.2
Mass, M (g)	1.20±0.13 ($0.0062L^3$)	1.078±0.119 ($0.0081L^3$)	2.969±0.527 $0.0113L^3$)	0.952±0.084 ($0.0035L^3$)
Muscle mass (g)	0.490±0.061 ($0.41M$)	0.517±0.139 ($0.48M$)	1.261±0.191 ($0.43M$)	0.516±0.112 ($0.55M$)
Wetted surface area (cm^2)	13.5±2.3 ($0.40L^2$)	13.0±2.1 ($0.50L^2$)	27.3±3.6 ($0.67L^2$)	12.1±2.4 ($0.29L^2$)
Lateral projected area (cm^2)	5.1±0.4 0.331	5.2±0.3 0.341	11.7±1.4 0.359	4.3±0.3 0.349
Distance of center of mass from nose (cm)	2.0±0.1	1.7±0.1	1.9±0.1	2.5±0.1
Acceleration coefficient	0.49	0.68	0.59	0.71

prove speed, acceleration, or maneuverability to evade an attack; (3) influence handling time. A fourth factor, prey response thresholds may vary among species, and by affecting the timing of prey responses, influence prey success. Therefore, the purpose of this study was to determine the effect locomotor form and performance and response thresholds on prey vulnerability, with the exception of prey selection and handling which are well researched (Deelder 1951; Hoogland et al. 1956; Mauck and Coble 1971; Gillen et al. 1981; Savitz and Jansen 1982; Moody et al. 1983).

Observations on captures of bluegill (*Lepomis macrochirus*) and fathead minnow (*Pimephales promelas*) by tiger musky (*Esox* sp.) suggest that strikes are directed towards the posterior of the body of bluegill prey (Moody et al. 1983). Unfortunately, these results are not definitive because only captured prey were sampled and other factors that could influence prey vulnerability were not recorded. I tested the hypothesis that spines and large body depth misdirect a predator strike away from the optimal center of mass target (Webb and Skadsen 1980; Webb 1984a) and thereby decreased prey vulnerability by comparing strike targets and captures in predator attacks on deep- and shallow-bodied spiny- and soft-rayed prey.

I tested the hypothesis that body and fin shape affect performance by applying theoretical models on thrust and drag to estimate relative performance capabilities and comparing these with observed swimming speeds and acceleration rates.

There are no comparative data on variations of prey response thresholds among species. Therefore, the null hypothesis was that there would be no differences. Any differences found would be expected to show reduced vulnerability for prey with lower response thresholds.

Materials and Methods

Observations were made on four teleost prey species attacked by largemouth bass (*Micropterus salmoides*): fathead minnow, tiger musky (*Esox* sp.; a hybrid cross between male *E. lucius* and female *E. masquinongy*), and two centrarchids, the bluegill sunfish and largemouth bass. Tiger musky and largemouth bass were obtained from hatcheries, fathead minnow from local bait stores, and bluegill by seining local ponds. All fish were acclimated to the experimental temperature of 15°C for at least 1 wk prior to use. The morphological features of the prey are summarized in Table 1. There were no significant differences in size among the largemouth bass predators attacking the four groups of prey. The dimensions (mean ± 2 SE; $N = 20$) of the predator were as follows: total length 23.3 ± 1.1 cm, mass 156.41 ± 21.8 g, maximum depth 6.4 ± 0.5 cm, maximum width 2.8 ± 0.2 cm, and maximum depth and width located 6.4 ± 0.4 cm from the nose.

The four prey species were selected to represent a range of forms that would be expected to affect prey vulnerability through bite-deterrent factors and locomotor performance. *Esox* was included because it has a fairly iniform depth over most of the body length and median fins are located towards the tail. Therefore, prey depth is not expected to influence predator targets for this species. The posterior location of the median fins ensures that these would not present miscues of apparent large depth or possible spines near the target. Fathead minnow has a fusiform body, somewhat deeper than *Esox* and with a soft-rayed fin over the center of mass. Largemouth bass has the same basic body shape as a minnow, but the fin over the center of mass is spiny. Bluegill sunfish have both a large body depth and spiny rays.

Locomotor performance can be measured in a number of ways depending on the propulsor and the type of activity. Escape responses involve body/caudal fin propulsive movements in fast-starts and sprints. These are defined as transient and periodic swimming, respectively, on the basis of the duration and repetition of propulsive movements (Weihs and Webb 1983). Transient and periodic swimming are further distinguished by the way the body is involved in generating thrust and in the dominant resistance to motion (Lighthill 1975; Weihs 1972, 1973; Webb 1977, 1984b; Weihs and Webb

1983). I determined the performance potential of the various forms using theories for thrust generation and resistance to obtain nondimensional factors for the propulsor (propeller) and muscle (motor).

In transient swimming, thrust is generated almost entirely by the portion of the body behind the center of mass. The thrust contribution of any point along the body is proportional to its added mass and the acceleration given to that mass. Added mass per unit length, m_a, is given by (Weihs 1972, 1973; Lighthill 1975)

$$(1) \quad m_a = \rho d^2/4$$

where ρ = density of water and d = body and fin depth.

The acceleration depends on the amplitude of lateral body movements, which increases along the body length as a quadradic function of distance from the center of mass (see figures in Hertel 1966; Weihs 1973; Webb 1976; Videler 1981). Therefore, to estimate the thrust potential of a body shape, I divided the body posterior to the center of mass into 10 strips. Each element was assigned a number from 0 at the center of mass to 10 at the trailing edge, and the square of this ranking number was used to weight the added mass. This gives an estimate of the expected relative contribution of each strip to total thrust. The sum of these values gives an estimate of the potential of the propeller to generate thrust, with units of mass.

Resistance in acceleration is proportional to the product of the mass of the body plus entrained water and the acceleration rate of the center of mass. Therefore, a dimensionless factor for the potential of the propeller to accelerate the body is obtained by the ratio of the propeller's thrust potential and the mass accelerated, equal to 1.2 × body mass.

The potential of the muscle motor to power the body depends on the muscle mass. The contribution of the motor to performance is therefore indicated by the percentage of muscle in the body.

The combined potential of motor and propeller contributions was obtained as their product and defined as the acceleration coefficient for the body. On this basis, the forms rank from lowest to highest potential to accelerate as follows: fathead minnow, bluegill sunfish, largemouth bass, tiger musky. Acceleration is maximal during the initial stages of a response, usually spanning the first tail beat. The mean acceleration was calculated for this period.

The same principles of relating thrust and drag can be applied for body form related to periodic swimming. Methods are described in detail elsewhere (see Bainbridge 1961; Webb 1975). Resistance power required is proportional to the product of total surface area and speed cubed, while thrust power is limited by muscle mass. Therefore, an estimate effect of the various forms on periodic swimming performance would be given most simply as the cube root of the ratio of muscle mass to surface area.

Predators were starved for 1 wk to ensure high motivation. Single predators were placed in an observation arena, 50 cm square and 10 cm deep. These dimensions do not interfere with strike interactions between predators and prey (Webb and Skadsen 1980; Webb 1984a). Prey were placed in four pens separated from the main arena by vertically closing doors. Predator and prey were left overnight in the arena and pens, respectively. The observation arena and side pens were kept at 15°C and were constantly illuminated by overhead fluorescent lights (0.2 $mW \cdot m^{-2}$).

The following morning, prey were introduced one at a time from a side pen selected at random. As prey were eaten, an additional prey was introduced. An experiment was terminated when the predator did not strike at a prey after 10 min.

Interactions between the predator and the prey were recorded on video tape and the tape was analyzed frame-by-frame (framing rate, 60 Hz). The predator's target along the prey body was measured either as the point at which the predator struck the prey or as the intersection point between the predator's strike trajectory and the prey's body prior to the start of an escape maneuver. Prey response thresholds were calculated as the apparent looming threshold or ALT (Webb 1980), defined as the rate of change of the angle subtended by the predator's cross-sectional silhouette as viewed by the prey at the start of its motor response (Dill 1974). It was calculated from

$$(2) \quad \mathrm{ALT} = \frac{4 \cdot V \cdot \mathrm{Sh}}{4 \cdot D^2 + \mathrm{Sh}^2}$$

where V = speed of the predator (centimetres per second), Sh = the mean of the maximum depth and width of the predator (centimetres), and D = the distance between the predator and the prey plus the distance of the maximum depth and width from the predator's nose (centimetres). Parameters V and D were measured at the beginning of the prey's motor response.

Prey response patterns, acceleration rates, and speeds were recorded for the startle responses and were analyzed to identify differences in motor response patterns. Escape speeds and trajectories were also recorded over 500 ms, after which most prey had stopped or been caught. Means and variance for tragectory angles were calculated as described by Batschelet (1966). Nonresponding prey were assumed to have such high thresholds that a prey motor response did not begin prior to the predator contacting the prey. Maximum likelihood estimates of means and variances of ALTs were calculated for truncated samples including these nonrespondants (Cohen 1961; Webb 1982).

The effectiveness of the prey in avoiding a predator was assayed by the predator's behavior. A predator may respond to an escape maneuver in one of three ways: (1) abort the interaction, (2) chase, or (3) bite. Predator response frequencies in these categories as well as eventual catch success were measured.

Results

Target

The target, defined as the intersection point between the predator's strike path and the prey body, did not differ significantly (Student's t-test; $p > 0.05$) from the center of mass for fathead minnow, largemouth bass, or tiger musky prey (Fig. 1). For bluegill prey, the mean target was $0.39 \pm 0.12\,L$ (L = length), significantly posterior to the center of mass at $0.30 \pm 0.01\,L$ (Student's t-test; $p < 0.05$). Targets were distributed over a greater portion of the body length of largemouth bass and bluegill prey, especially the latter (Fig. 1). An expected normal distribution along the body for strikes centered on the center of mass was calculated for each prey from mean and standard deviation of the observations (Sokal and Rohlf 1981). Strike targets on largemouth bass were neither significantly different from the expected normal distribution nor the observed distribution of targets on the soft-rayed species (chi-square; $p > 0.05$). Therefore, largemouth bass

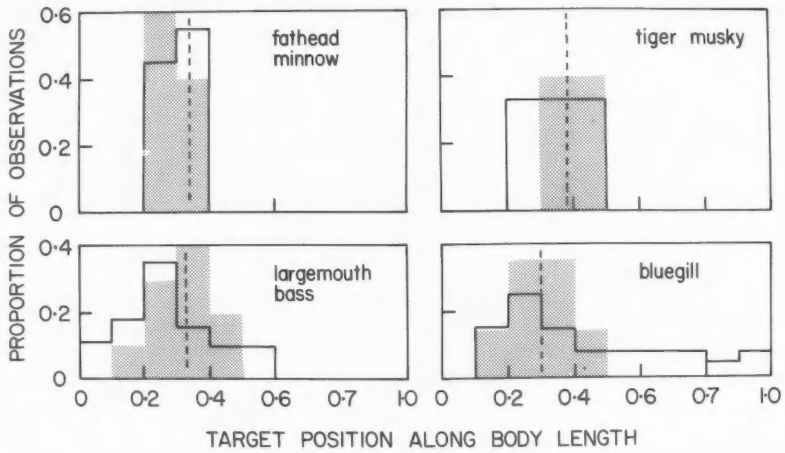

FIG. 1. Frequency distributions showing percentages of predator strike targets at various positions along the prey body length and those leading to capture (stipple). The vertical broken lines show the average location of the prey center of mass.

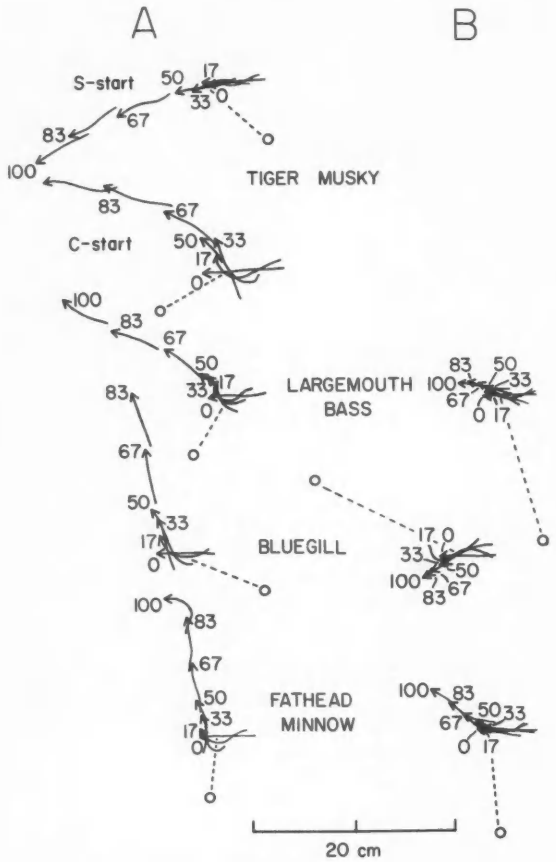

FIG. 2. Tracings of the center line of prey during escape attempts to illustrate the various escape patterns. (A) High-level responses; (B) low-level responses. Open circles and broken lines show the initial position and strike trajectory, respectively, of the predator's mouth.

spines are not shown to substantially influence the strike target of largemouth bass predators. In contrast, expected and observed distributions of targets were significantly different (chi-square; $p < 0.05$) for bluegill prey, showing that large body depth (perhaps combined with spines) affected predator targets.

The observed distributions of strike targets and of targets resulting in prey capture were similar for tiger musky, fathead minnow, and largemouth bass (chi-square; $p < 0.05$). Successful predator strikes intercepted prey near the center of mass of all four prey species. Therefore, the shift in strikes from the center of mass region of bluegill prey is shown to decrease prey vulnerability.

Prey Responses

Four prey response patterns were observed: (1) no escape response prior to predator contact, (2) low performance responses associated with small-amplitude body movements, (3) high-performance, large-amplitude accelerations, with the body bent into C-shapes, and (4) high-performance S-starts seen only in tiger musky and involving small-amplitude body movements and S-shaped postures (Fig. 2 and 3; Table 2).

From 4 to 24% of prey did not respond to strikes, with fathead minnow having the greatest proportion of nonrespondents (Table 2). Approximately half of all responses to the predator were high-level C-starts; low-level responses were less common (28–45%). In tiger musky, only high-level responses occurred, with S-starts and C-starts in similar numbers (Table 2).

In low-level responses, prey accelerated at low rates to reach maximum speeds of 40–50 $cm \cdot s^{-1}$ within about 150 ms (Fig. 3A, 3B, 3C). Prey usually decelerated after the initial acceleration, although largemouth bass showed a second acceleration to 63 $cm \cdot s^{-1}$ after 400 ms (Fig. 3B). Escape trajectories subtended small angles, typically less than 40° to the original body axis (Fig. 3E, 3F, 3G).

In high-level C-start and S-start responses, prey accelerated at higher rates to reach speeds of 66–108 $cm \cdot s^{-1}$ within 150–200 ms (Fig. 3A, 3B, 3C, 3D). Fathead minnow reached their maximum speed of 66 $cm \cdot s^{-1}$ after 33 ms. The other prey

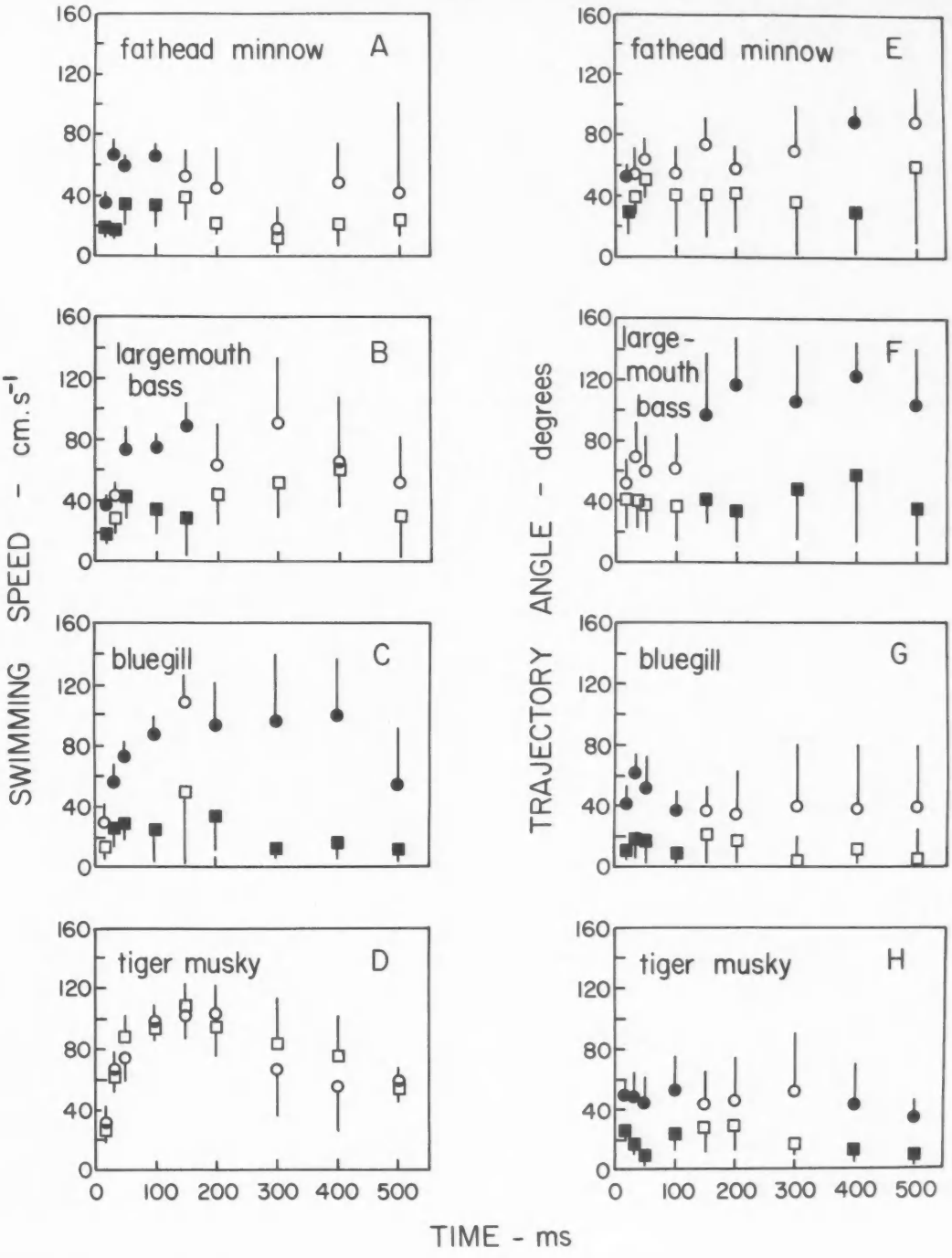

FIG. 3. Performance of prey during escape responses. (A–D) Escape speeds; (E–H) escape angles, measured from the initial prey body axis. Circles represent high-level responses and squares low-level responses for fathead minnow, largemouth bass, and bluegill. These symbols represent C-starts and S-starts, respectively, for tiger musky. Significant differences (Student's t-test; $p < 0.05$) in performance at any time are shown by solid symbols. Vertical lines show ± 2 SE.

TABLE 2. Prey response patterns to strikes by largemouth bass.

Prey	Fathead minnow	Largemouth bass	Bluegill	Tiger musky
Number of nonrespondents	7 (24%)	2 (7%)	5 (18%)	1 (4%)
Number of low-level type 1 responses	8 (28%)	13 (45%)	9 (32%)	—
Number of high-level type 2, C-start response patterns	14 (48%)	14 (48%)	14 (50%)	14 (50%)
Number of S-start response patterns	—	—	—	13 (46%)

TABLE 3. Frequencies of largemouth bass predator responses elicited by escape behavior of four species of prey. Frequencies are shown as proportions of the total responses (abort, chase, and bite) summed for both high- and low-level prey responses. Catches are secondary behaviors that may occur as a result of initial or subsequent bites during chases. There are shown as proportions of total strikes for the two levels of prey response.

	Fathead minnow		Largemouth bass		Bluegill sunfish		Tiger musky	
Predator response	High-level responses	Low-level responses	High-level responses	Low-level responses	High-level responses	Low-level responses	C-start responses	S-start responses
Abort	0.23	0.079	0.33	0.23	0.38	0.19	0.43	0.33
Chase	0.15	0.17	0.10	0.15	0.14	0.081	0	0.067
Bite	0.27	0.096	0.15	0.026	0.19	0.027	0.067	0.10
Catches	0.096	0.038	0.077	0	0.027	0.027	0	0.067
N	52		39		37		30	

species attained similar speeds in this time, but continued to accelerate for 150–200 ms. Fathead minnow and tiger musky decelerated after reaching peak speeds, but the two centrarchids tended to sustain their high speeds for 200–400 ms. Acceleration rates and speeds of tiger musky C-starts and S-starts were similar (Student's *t*-test; $p < 0.05$).

Average prey speeds were calculated for the chases that occurred. Maximum speeds recorded in chases were 80.7 ± 15.7 $cm \cdot s^{-1}$ ($n = 11$) for fathead minnow, 96.4 ± 14.4 $cm \cdot s^{-1}$ ($n = 7$) for largemouth bass, 100.6 ± 21.21 $cm \cdot s^{-1}$ ($n = 3$) for bluegill and 136 $cm \cdot s^{-1}$ ($n = 2$) for tiger musky. These were 3 to 15% higher than the average maximum speeds recorded in responses where predators did not chase. However, the number of chases was small (Table 3) and differences in speed were not statistically different between chases and other responses.

Escape trajectories for tiger musky S-starts, like the low-level responses of other species, subtended small angles, typically less than 30° to the original body axis (Fig. 3H). Otherwise the high acceleration rates of C-start responses were associated with large escape trajectory angles (Fig. 3E, 3F, 3G), probably the result of body recoil due to unbalanced side forces (Weihs 1973).

Effects of body and fin form on performance are only relevant if prey function at maximum speeds and acceleration rates. Otherwise, form permits but does not limit performance (Webb 1984a). Maximum performance did not occur in the low-level responses. Similarly, the pattern of deceleration in some prey and second, lower accelerations in others show that prey did not usually reach maximum speeds, presumably because prey were not usually chased (Webb 1981). Nevertheless, high levels of performance would be expected initially to remove prey rapidly from the predator's strike trajectory,

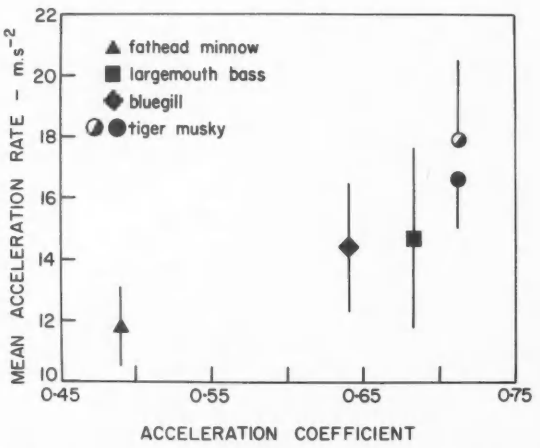

FIG. 4. Relationship between mean acceleration rate and acceleration coefficient during high-level startle responses of four species of prey attacked by largemouth bass. The half-solid symbol for tiger musky represents S-starts and the solid symbol C-starts.

and are ensured because the startle response is an all-or-none maximum fast-start (Eaton et al. 1977). Therefore, results for acceleration in high-level responses can be used to examine the influence of body form on performance. It was found that mean acceleration rates increased with the acceleration coefficient (Fig. 4).

Prey Response Threshold

Prey response thresholds (ALTs) for low-level responses

TABLE 4. Results of ANOVA and multiple linear regression analysis of the frequency of predator response choices to prey acceleration performance and response threshold (ALT).

	ANOVA					Multiple regression			
Predator response	Source	Degrees of freedom	Sum of squares	Mean square	r^2	Significance	Variable	Partial correlation coefficient	Significance
Abort	Regression	2	589.24	294.62	0.64	0.08	Acceleration	0.76	0.05
	Error	5	338.46	67.69			ALT	0.0004	0.99
	Total	7	927.70						
Chase	Regression	2	152.61	76.31	0.66	0.07	Acceleration	−0.81	0.03
	Error	5	80.23	16.05			ALT	0.65	0.12
	Total	7	232.84						
Bite	Regression	2	443.30	221.65	0.90	0.003	Acceleration	−0.38	0.40
	Error	5	49.30	9.86			ALT	0.94	0.002
	Total	7	492.60						
Catch	Regression	2	25.86	12.93	0.30	0.42	Acceleration	0.05	0.91
	Error	5	61.72	12.34			ALT	0.48	0.28
	Total	7	87.58						

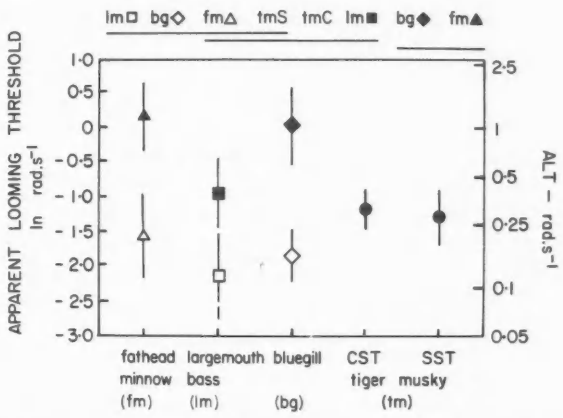

FIG. 5. Apparent looming thresholds of prey in response to attacks by largemouth bass. Solid symbols are for high-level responses and open symbols are low-level responses. Mean ± 2 SE are shown. Results of comparisons for significant differences are shown above; lm, largemouth bass; bg, bluegill; fm, fathead minnow; tm, tiger musky.

varied from 0.12 to 0.16 rad·s^{-1} (Fig. 5) and did not differ significantly between fathead minnow, largemouth bass, and bluegill (Scheffe's method for multiple comparisons; Sokal and Rohlf 1981). Maximum likelihood means for ALTs of high-level responses were greater than for low-level responses, and ranged from 0.31 to 1.15 rad·s^{-1}. S-starts by tiger musky were associated with a mean ALT of 0.27 rad·s^{-1} which was not significantly different from the 0.31 rad·s^{-1} for C-start responses by this species (Student's t-test; $p < 0.05$).

Predator Responses to Prey Escape Maneuvers

Predators have three options in responding to escape attempts by prey: (1) bite at prey, (2) chase, or (3) abort the interaction. Some bites will also be effective in catching prey.

The frequencies of abort, chase, and bite responses of predators elicited by prey responses are shown in Table 3. Multiple linear regression analysis was used to determine relationships between prey acceleration performance and ALT and the frequency of each predator response (Table 4).

The frequencies of predator choices to abort or to chase prey are not fully described by prey acceleration and ALT ($0.1 < p < 0.05$; Table 4). Many additional factors could contribute to predator decisions, for example experience. Nevertheless, prey acceleration explained most of the variation in predator decisions to abort an attack or to chase prey. The frequency of bites was well described by prey acceleration and ALT ($p < 0.05$), but prey ALT was more important in determining whether or not a predator would bite. Catches were relatively rare, and were not significantly related to prey escape performance or ALT. However, bites and catches were related. It is important to note that the relations between ALTs and bites could be spurious if ALTs were correlated with body depth and spines. However, there was no correlation between relative body depth and ALT. Nevertheless, the effect of body form on the predator's target selection undoubtedly increased variability in the data and reduced the correlation coefficient.

Therefore, Tables 3 and 4 show that the probability of a predator terminating an attack increased as prey acceleration capabilities improved. In this respect, higher performance correlated with increased effectiveness of prey escape behavior. The frequency of predator choices to chase declined primarily with increasing prey performance, so that again higher performance increased escape effectiveness. In contrast, the frequency of predator bites depended mainly on the response threshold, since ALT (more distant and/or slower predators) resulted in fewer bites and captures.

Discussion

Acceleration performance varied with prey body form, and higher acceleration rates correlated positively with higher proportions of aborted strikes and inversely with the frequency of chases. Prey behavior can be considered most effective in minimizing vulnerability when it influences a predator to abort a strike. Consequently, prey form and associated locomotor performance reduce vulnerability by deterring predators from continuing to attack and reducing the chance of a chase. This correlation between body form and performance with prey

success contrasts with the situation for predators, where body form has remarkably little effect on strike performance (Webb 1984a).

Prey shape also influences vulnerability by modifying bite targets of predators. It is already known that predators strike fusiform soft-rayed prey in the midbody region, while deep-bodied, spiny prey are struck caudally (Moody et al. 1983). Moody et al. (1983) also showed that strike success was lower in the latter situation, and suggested that this was due to spines misdirecting attacks from a target near the center of mass. However, in the present experiments the spines of largemouth bass prey were not shown to substantially influence strike targets of the predators, implying that large body depth is the more important factor affecting predator target selection. However, captures of all prey are most likely for strikes in the region of the center of mass. Therefore, misdirection of strikes from the expected optimum target is shown to be a mechanism whereby body shape reduces prey vulnerability.

Body form characteristics are not the only factors affecting the outcome of a predator–prey interaction; the timing of the prey response, determined by the response threshold, is also important (Webb 1982). Lower prey ALTs contributed to reducing the frequency of predator chases (Table 4), but were most important in deterring bites. Thus, predators were less likely to bite prey with lower response thresholds.

The different contributions of acceleration performance and ALT to the frequencies of predator behavior choices probably relate to the different times available for predator decisions. Predators bite when they are moving fast and/or are close to prey, i.e. when the anticipated closure time with the target is small. Predator response latencies (Webb 1984c) and the time required to bite (Lauder 1983) are relatively long, so that there probably would be insufficient time for predators to use prey escape performance levels in making behavior choices. Then the decision to bite is most likely to depend on the predator's anticipated closure time. Since prey with higher ALTs permit predators to get closer before responding, predators would be expected to attempt to bite such prey more frequently.

In contrast, longer closure times correlate with lower ALTs, i.e. prey respond to slower and/or more distant predators. Under these circumstances secondary information on performance could be more easily utilized, and chases or aborted attacks would occur.

Prey responses, as measured by ALTs, varied among species. I know of no theory or substantive observation that explains this variation. Furthermore, acceleration performance and ALT are inversely related for high-level responses (Fig. 4 and 5; $r = 0.87$; $p < 0.05$). This is counterintuitive, for it would seem more likely that slower prey could offset low performance with lower response thresholds. Instead, prey with high acceleration performance further reduce their vulnerability with low response thresholds. This suggests that substantial costs may be associated with escape behavior, relating to some (unknown) feature of the prey's interactions with its habitat. Following Triesmann (1975), one such cost might be related to foraging patterns. Fish feeding on small items must actively forage for longer periods of time compared with those eating larger items. In such circumstances, premature predator escape responses would have larger consequences on fish eating smaller items because interruption of feeding would immediately affect the amount of energy acquired. In contrast, fish eating larger items less frequently would be less likely to have their rate of food consumption reduced by escape behavior. This is consistent with the tendency for the prey species with the lower thresholds (e.g. tiger musky) to eat large food items compared with those with higher ALTs tending to eat small items (e.g. fathead minnow) (Scott and Crossman 1973). In addition, nonlocomotor predator avoidance adaptations would be expected among the slower prey with higher response thresholds. Schooling in species such as minnows is one alternative. Others include deterrent affects of body shape and spines such as those of the centrarchids.

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Egg Loss from the American Lobster, *Homarus americanus*, in Relation to Nemertean, *Pseudocarcinonemertes homari*, Infestation

Alan Campbell

Invertebrates and Marine Plants Division, Fisheries Research Branch, Department of Fisheries and Oceans, Biological Station, St. Andrews, N.B. E0G 2X0

and John Brattey

P.O. Box 472, St. Andrews, N.B. E0G 2X0

Campbell, A., and J. Brattey. 1986. Egg loss from the American lobster, *Homarus americanus*, in relation to nemertean, *Pseudocarcinonemertes homari*, infestation. Can. J. Fish. Aquat. Sci. 43: 772–780.

The relationship between nemertean (*Pseudocarcinonemertes homari*) infestaton and egg loss from ovigerous American lobsters, *Homarus americanus*, trapped near Grand Manan, New Brunswick, was investigated during 1980–83. The proportion of lobster eggs lost each month was variable, but generally increased to a maximum of 0.38–0.43 at the end of each of the three egg incubation periods. Up to 6.3% of the newly ovigerous lobsters tagged (N = 1413) during July–October 1982 has lost all their eggs by April–July 1983. Most ovigerous lobsters (74%) were infested with *P. homari*, but many lobsters had low mean densities of nemerteans (<2/1000 lobster eggs). There was a significant but low correlation between *P. homari* densities and the proportion of eggs lost; however, egg losses could not be attributed solely to *P. homari*. Egg loss did not differ significantly between uninfested and nemertean-infested lobsters during each of the three egg incubation periods. The few lobsters that acquired high densities (>4) of *P. homari* during the early stages of egg incubation appeared to suffer extensive or complete egg mass destruction. However, most lobsters maintained low densities (<2) of nemerteans and hatched most (>60%) of their eggs.

On a examiné en 1980–1983 la relation entre les infestations de némertiens (*Pseudocarcinonemertes homari*) et la perte des oeufs chez des homards ovigères de l'espèce *Homarus americanus* qui ont été capturés près de Grand Manan au Nouveau-Brunswick. La proportion d'oeufs perdus chaque mois était variable, mais augmentait généralement jusqu'à un maximum de 0,38–0,43 à la fin de chacune des trois périodes d'incubation des oeufs. Jusqu'à 6,3 % des homards nouvellement ovigères, qui avaient été marqués (N = 1413) de juillet à octobre 1982, avaient perdu la totalité de leurs oeufs à l'époque d'avril–juillet 1983. La plupart des homards ovigères (74 %) étaient infestés par *P. homari*, mais un grand nombre d'entre eux transportaient des populations moyennes faibles de némertiens (<2/1000 oeufs de homards). On a observé une corrélation significative, mais faible, entre les densités de *P. homari* et la proportion d'oeufs perdus; toutefois, on n'a pu uniquement attribuer les pertes d'oeufs à *P. homari*. La mortalité des oeufs ne différait pas de façon significative chez les homards infestés et les homards non infestés par des némertiens, au cours de chacune des trois périodes d'incubation des oeufs. Les quelques homards infestés par des populations denses (>4) de *P. homari* durant les étapes initiales d'incubation des oeufs semblaient subir une destruction importante ou complète de la masse d'oeufs. Toutefois, chez la plupart des homards, la densité de némertiens était faible (<2) et la plupart de leurs oeufs (>60 %) ont pu éclore.

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The discovery of *Pseudocarcinonemertes homari* Fleming and Gibson, 1981 on the American lobster, *Homarus americanus*, in 1978 (Aiken et al. 1983) led to a series of studies on the nemertean's taxonomy (Uhazy et al. 1985), biology (Aiken et al. 1985; Waddy and Aiken 1985), and geographic distribution and seasonal occurrence (Brattey et al. 1985). Although lobster egg destruction by *P. homari* was noted, none of these studies assessed the impact of this nemertean on the reproductive potential of *H. americanus* populations. Increased exploitation of the lobster population in the Bay of Fundy since 1974 (Campbell and Duggan 1980; Campbell 1984) has caused some concern that the total egg production of lobsters in the area could be reduced (Campbell and Robinson 1983). In addition, a recent geographic survey found that a large proportion of ovigerous lobsters in the Bay of Fundy, especially near Grand Manan, were infested with *P. homari* (Brattey et al. 1985). Here we examine lobster egg loss in relation to *P. homari* infestation during three successive egg incubation cycles of ovigerous *H. americanus* near Grand Manan.

Materials and Methods

Sampling

Ovigerous lobsters were trap-caught at depths of 6–230 m east and south of Grand Manan, New Brunswick, during most months from November 1980 to August 1983. On removal from the traps, the lobsters were immediately sampled by one of two methods. (1) Whole lobster samples: intact ovigerous females (N = 249) were collected from November 1980 to September 1982 (Brattey et al. 1985), plus nine lobsters in July 1983, and placed individually in polyethylene bags. (2) Pleopod egg samples: all eggs were removed from the pair of pleopods on the second (anterior) abdominal segment of 552 lobsters captured from March 1982 to August 1983; the ovigerous lobsters captured during July 1982 – July 1983 were also tagged (see below) before being returned to sea. Of the tagged lobsters that were subsequently recaptured, seven had an additional egg sample removed from the pair of pleopods on the third abdominal segment. This allowed egg development, egg loss, and nemertean abundance to be monitored on individual lobsters over several months. All samples were placed in an insulated cooler and frozen within 6 h at −20°C for storage. The following details were recorded for each lobster: date, depth, and location of capture and the carapace length (CL), from the base of the eye socket to the posterior margin of the carapace parallel to the mid-dorsal line, measured with a vernier caliper to the nearest millimetre. All samples were taken by one or two well-trained Department of Fisheries and Oceans (DFO) personnel.

Tagging

We tagged ovigerous lobsters (1) to determine the percentage of ovigerous females which extruded eggs during summer 1982 and subsequently lost them during the 9- to 12-mo incubation period and (2) to monitor egg loss and nemertean abundance on individual tagged lobsters by taking pleopod egg samples between the time of release and recapture. However, it was not possible to sample pleopod eggs of all tagged lobsters at release; some females were sampled only at recapture. Ovigerous lobsters (N = 2139) were tagged and released off Grand Manan from July 1982 to July 1983. Only those lobsters with newly extruded eggs released during July (N = 3), August (360), September (650), and October (397) 1982 were used to calculate total egg loss. To estimate the percentage of tagged females that lost all their eggs each month, we used $N/T \times 100$, where N = number of tagged females captured per month that were no longer ovigerous and T = total recaptures per month (including both ovigerous and nonovigerous females). Each ovigerous lobster was tagged with a "sphyrion" spaghetti tag (Scarratt and Elson 1965) by trained DFO personnel. The tag anchor was inserted into the dorsal musculature between the carapace and abdomen. The tagged lobsters were usually returned to the water as close as possible to the capture site <10 min after being removed from the traps. Information recorded for each tagged lobster included CL, tag number, location, depth, and date of capture. During the closed fishing season (July to mid-November), tagged lobsters were recaptured by DFO personnel on board a lobster fishing boat chartered during 23 July – 2 November 1982 and 21 July – 26 August 1983. During the open fishing season (mid-November 1982 – June 1983), 10 North Head, Grand Manan, commercial lobster fishermen aided DFO personnel in recapturing tagged lobsters. The fishermen were provided with vernier calipers and asked to keep records of recapture tag numbers, sex, CL, and presence or absence of eggs. A reward of up to $5.00 was paid for information on each tag recapture. In addition, a DFO representative collected tag recapture information from the fishermen each day; their cooperation was excellent. Also, there was greater than 96% agreement between CL measured at release and recapture which helped verify the accuracy of the information provided by the fishermen.

Interpretation of the tag-return data should be considered with caution because lobsters can be trapped selectively. Differences in open fishing seasons can cause trap efficiency to vary from one area to another because the activity and physiological condition of lobsters may vary with season (McLeese and Wilder 1958; Elner 1980). Consequently, there may have been a differential catchability between tagged ovigerous and nonovigerous females. Although difficult to determine, the exact catchability of females in each reproductive condition was probably not a major problem for this study, since many mature males and ovigerous and nonovigerous females were caught in baited traps by fishermen in the area throughout 1982–83. Also, traps were designed to be nonselective for lobsters greater than 94 mm CL (Campbell and Duggan 1980).

TABLE 1. Proportions of the total lobster egg mass carried on each lateral pair of pleopods and densities of nemerteans on each pleopod pair compared with the total egg mass of each lobster. SE = standard error, N = number of lobsters sampled in February–September 1983 and July 1983.

	Proportion of total fecundity (N = 130)		Density[b] (nemerteans/1000 eggs) (N = 108)	
Pleopod pair[a]	Mean	SE	Mean	SE
1	0.06	0.002	0.317 A	0.038
2	0.24	0.003	0.481 AB	0.038
3	0.28	0.003	0.624 B	0.041
4	0.25	0.003	0.567 B	0.039
5	0.17	0.004	0.313 A	0.029
Total	1.00		0.598 B	0.053

[a]From anterior to posterior of lobster abdomen.

[b]Geometric mean of infested lobsters only. Means followed by same letter are similar ($p > 0.05$) using Student-Newman-Kuels test after $\log_{10}$ transformation.

Nemerteans

Whole lobsters and pleopod egg samples were thawed and *P. homari* were removed and counted using methods described by Brattey et al. (1985). Prevalence is the percentage of ovigerous lobsters infested with nemerteans and density is the mean number of nemerteans per 1000 lobster eggs per infested lobster (Margolis et al. 1982). To investigate differences in density either between pleopod pairs, between monthly samples, between lobster size groups, or between proportion egg loss groups, we used one-way analysis of variance and the Student–Newman–Keuls test (Kim and Kohout 1975) after $\log_{10}$ transformation. Only the geometric mean densities are shown which are the retransformed means of the transformed variables. To investigate differences in prevalence between monthly samples or between lobster size groups, the G-test was used (Sokal and Rohlf 1969).

TABLE 2. Relationship between lobster carapace length and number of newly extruded and old eggs for whole egg masses and eggs on the second or third pairs of pleopods based on the regression equation $\log_e$ (egg number) $= a + b \log_e$(CL). R = correlation coefficient, SE = standard error of b, N = sample size. New eggs are those newly extruded without eye spots and were collected August–September. Old eggs had well-developed eye spots and were collected June–July–August.

Year	Egg type	Regression constants a	b	R	SE	CL (min.–max.)	N
			Whole egg mass				
1981	New	−6.286	3.518	0.759	0.692	108–138	21
1982	New	−5.416	3.330	0.929	0.231	105–164	35
1981–82	New	−5.452	3.341	0.881	0.237	105–164	56
1980–83	Old	−5.939	3.357	0.768	0.278	96–157	91
			Second pleopod pair				
1982	New	−5.631	3.078	0.889	0.275	105–164	35
1982–83	Old	−6.151	3.084	0.535	0.576	85–188	260
			Third pleopod pair				
1982	New	−5.906	3.165	0.929	0.220	105–164	35

Lobster Fecundity

After all nemerteans were removed, the lobster eggs were preserved in 5% formalin solution ≥24 h. A subsample of 10 preserved eggs was taken and the longest and shortest axes of the darkly pigmented crescent of the eye of each egg were measured to the nearest 0.01 mm; the two measurements were averaged to obtain the eye index, a measure of egg development (Perkins 1972). All preserved eggs were then oven-dried at 70°C for 48 h, and the dried egg samples were rubbed over a screen seive (0.25 mm) to separate the eggs from extraneous material. Each sample (whole egg mass or pleopod egg sample) was weighed, and eggs in three weighed subsamples were counted to estimate the total number of eggs per sample. Error associated with this method was estimated at <1% when compared with counting the total number of eggs from 10 samples.

To estimate (1) the proportion of the total egg mass carried on each of the five pairs of pleopod and (2) whether these proportions changed with lobster size or collection date, we counted the eggs on each of the five pairs of pleopods on 130 whole egg masses collected from February 1982 to September 1982 and July 1983.

The relationship between carapace length (X) and the number of eggs per sample (Y) was approximated, using a linear equation of the form $\log_e Y = a + b \log_e X$. The constants a and b were estimated by the linear least squares method after transforming X and Y by $\log_e$ for newly extruded eggs obtained only during August–September 1981 and 1982 for either the whole egg masses or the pleopod egg samples. The fecundity estimates from whole masses of newly extruded eggs for 1981 and 1982 were compared using analysis of covariance (Engleman 1981) after $\log_e$ transformation of the data for the same size range for which data were available. Since there were no significant differences ($p > 0.05$) in slopes and elevations between the two equations, the 1981 and 1982 results were combined giving one equation relating numbers of newly extruded eggs and CL; this equation was used to estimate numbers of newly laid eggs for the 1980 extrusion period. To estimate the number of newly extruded eggs on the second pleopod pair for the 1981 extrusions, the whole egg mass fecundity equation for 1981 was multiplied by 0.24, since the second pleopod pair carries about a quarter of the total egg mass (Tables 1, 2).

Lobster Egg Loss

Estimates of the egg loss for each ovigerous female were based on the difference in numbers of newly extruded eggs and numbers of developing eggs during each of the three incubation periods using the following formula: $P = 1 - Z/V$, where P = proportion egg loss, Z = number of observed developing eggs, and V = predicted mean number of newly extruded eggs for the equivalent CL (for each pleopod pair or whole egg mass). Only whole egg mass fecundity estimates were used for the 1980 extrusion (i.e. March 1980 – August 1981). A combination of pleopod egg samples and whole egg mass samples was used for fecundity estimates for the 1981 and 1982 extrusions.

Two-way analysis of variance (Kim and Kohout 1975) was used to compare egg losses (P) from nemertean-infested and uninfested lobsters between monthly periods for each of the three egg incubation cycles after the P's were arcsine transformed.

The egg loss estimates for individual lobsters should be considered with caution because the mean fecundity values calculated for lobsters with old and new eggs were based on different individuals from the population. Since there was a natural variation about the mean fecundity at any CL, a few lobsters were recorded with negative egg loss, i.e. more (not fewer) older eggs were observed than the estimated mean number of newly laid eggs at a particular CL. However, for a population of lobsters, the method used was a reasonable approximation. Unfortunately, there was no other field method available to estimate egg loss from lobsters in the wild. Determining egg mortality through counting accumulated dead eggs or egg shells (e.g. Wickham 1979a, 1979b) was not reliable for

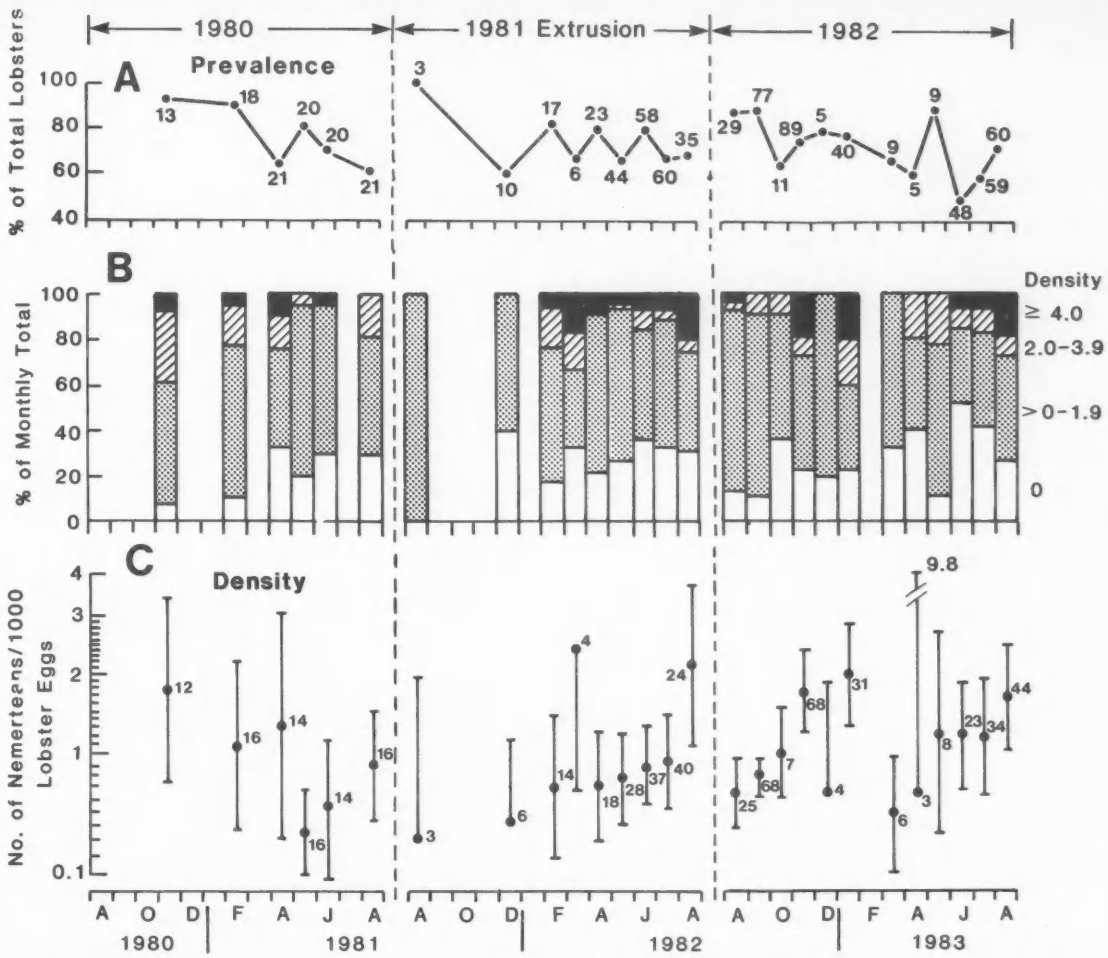

FIG. 1. Seasonal changes in *P. homari* infestation of ovigerous lobsters caught near Grand Manan during three egg incubation periods. (A) prevalence of nemertean worms; (B) frequency distribution of nemertean densities expressed as a percentage of total sample sizes per month, unshaded area = no nemerteans, stippled >0−1.9, hatched = 2.0−3.9, and black ≥4.0 nemerteans/1000 eggs; (C) density of nemerteans on infested lobsters. Points are means, vertical lines are 95% confidence intervals, and numbers are sample sizes.

lobsters, since dead eggs were washed or brushed away from the egg mass by pleopod movement and grooming by chelate pereiopods (Aiken et al. 1985).

Estimating egg loss by comparing CL−fecundity regressions from whole lobsters collected from the wild at the beginning and end of the egg incubation period has several disadvantages. The method involves (1) removal of whole ovigerous lobsters, thus depleting the brood stock, and (2) determining fecundity from different individuals at different periods. In contrast, the pleopod egg sampling method does not remove whole ovigerous females from the fishery, and large numbers of individuals can be sampled at any one time. Ideally, pleopod egg samples should be obtained from tagged recaptured individuals in the wild throughout the egg incubation period to monitor the densities and stages of nemerteans and/or other egg-fouling biota, and lobster egg development and loss. Unfortunately, this method can be difficult and costly, since many ovigerous lobsters must be tagged and pleopod egg samples obtained at the beginning to ensure sufficient recaptures towards the end of the egg incubation period.

Results

Pleopod Samples

The second, third, and fourth pairs of pleopods carried most (77%) of the total lobster egg mass (Table 1). The timing of the monthly egg sampling and the size of lobster did not significantly affect (ANOVA, $p > 0.05$) the mean proportion of eggs carried on the second pair of pleopods; consequently all data were combined for each pair of pleopods (Table 1). There were no differences ($p > 0.05$) in numbers of nemerteans per 1000 lobster eggs between the second, third, and fourth pairs of pleopods and total egg mass (Table 1). There were significantly fewer ($p < 0.05$) nemerteans per 1000 lobster eggs on the first and fifth pair of pleopods than on the other three pleopod pairs (Table 1), which suggests that nemerteans tend to avoid the periphery of the egg mass. These results indicate that samples from the second and third pair of pleopods were representative for monitoring relative changes in nemertean density and lobster fecundity.

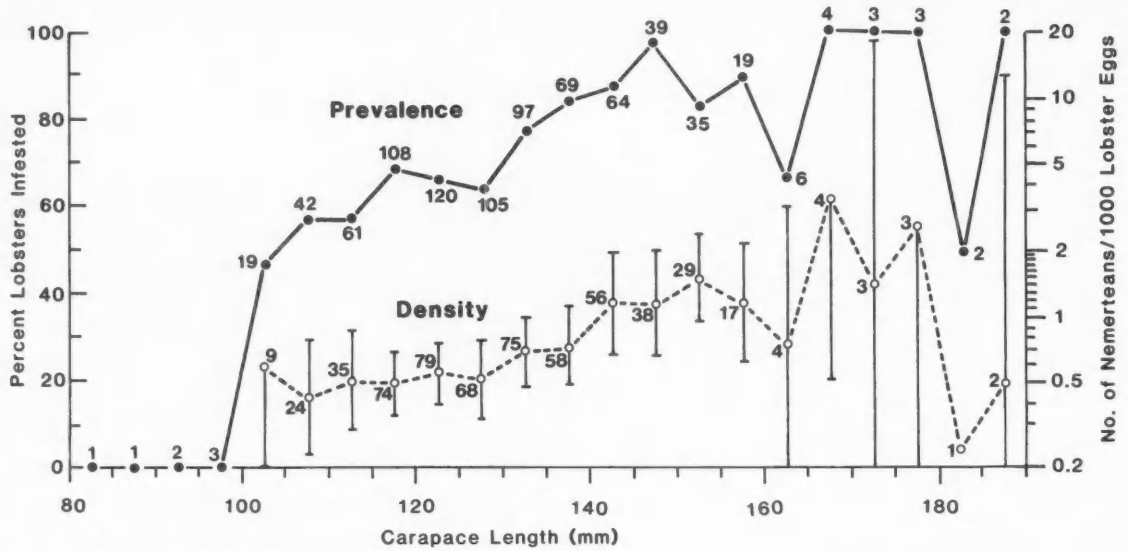

FIG. 2. Relationship between ovigerous lobster size (CL) and the prevalence and density of *P. homari*. Data from three egg incubation periods were combined. Points are means, vertical lines are 95% confidence intervals, and numbers near points are numbers of lobsters sampled for each 5-mm CL group. Of the 810 lobsters sampled, 5 had unknown CL.

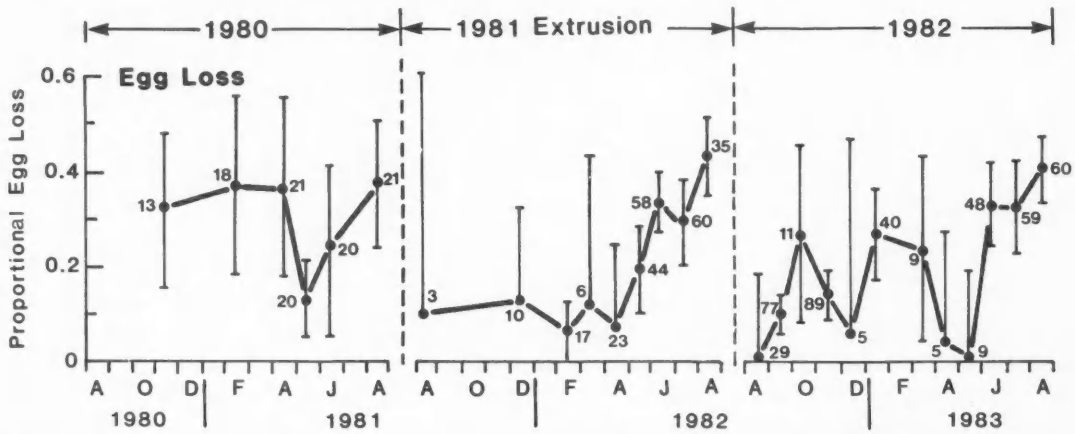

FIG. 3. Seasonal changes in mean egg loss during three incubation periods for all lobsters sampled near Grand Manan. Numbers near points are sample sizes.

Nemerteans

Seasonal occurrence

Prevalence of nemerteans was highest in the early stages of lobster egg development and, in general, declined until the late stages of egg development during each of the three egg incubation periods (Fig. 1A). No seasonal trends in mean density were evident and there was considerable variation in the number of nemerteans found within each month. Few (≤20%) lobsters had high densities of nemerteans (≥4.0 nemerteans/1000 eggs) during the three egg incubation periods (Fig. 1B). Monthly mean densities varied between 0.30 and 2.37 nemerteans/1000 eggs (Fig. 1C).

Host size

Overall, the arithmetic mean CL of ovigerous lobsters was 130 mm (85–188 mm). There were no significant differences (ANOVA, $p < 0.05$) in mean CL between months, so host size should not have influenced the seasonal comparisons between nemertean prevalence, density, or proportional egg loss.

Prevalence significantly increased (G-test, $p < 0.01$) with increasing lobster size but nemertean density and CL were not significantly correlated ($R = 0.04$; $p > 0.05$) (Fig. 2). Nemertean density ranged from 0.25 to 3.42 but there were no significant differences (Student–Newman–Keuls test, $p > 0.05$) in densities between size groups of lobsters (Fig. 2).

Lobster Egg Loss

Fecundity

The curvilinear relationships between fecundity and CL were highly correlated (Table 2). Analyses of covariance, within the

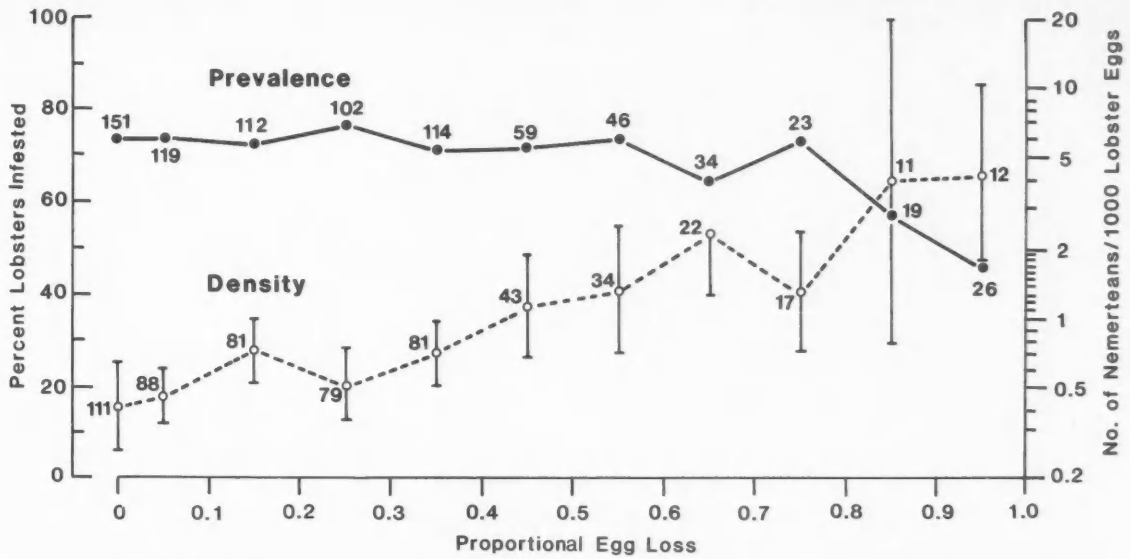

FIG. 4. Prevalence and density of *P. homari* on ovigerous lobsters in relation to egg loss groups of 0.1. Data from three egg incubation periods were combined. Points are means, vertical lines are 95% confidence intervals, and numbers near points are numbers of lobsters sampled for each 0.1 egg loss group.

size range examined, indicated that there were no differences between years ($p > 0.05$) in slopes and intercepts of the regression lines for newly extruded eggs (August–September) and for old eggs (June–August); consequently, data for all years were combined giving two equations, one for old and one for new eggs (Table 2). Comparisons of regression lines using analysis of covariance between new and old eggs indicated no significant differences ($p > 0.05$) between slopes, but there were significant differences ($p < 0.01$) between adjusted means (Y-intercepts); these results suggest that egg loss between egg extrusion and hatching was similar for most female sizes. Overall, the average proportional egg loss between egg extrusion and hatching within the size range examined was 0.34 for whole egg samples and 0.39 for the pleopod egg samples.

Seasonal trends

There were significant differences (ANOVA, $p < 0.01$) in mean egg loss between months for both the nemertean-infested and uninfested lobsters. However, there were no significant differences ($p > 0.05$) in mean egg loss between infested and uninfested lobsters during the three egg incubation periods; consequently, monthly egg losses for nemertean-infested and uninfested lobsters were combined (Fig. 3). Mean egg loss between some months was variable perhaps due to small sample sizes in some months; however, mean egg loss generally increased to a maximum at the end of each incubation period in August (Fig. 3).

Egg loss during July and August of each year may have included some eggs that hatched. The mean eye index values were high with maximum values well above the egg hatching threshold (Table 3). Although Perkins (1972) considered an eye index of 560 μm a value at which *H. americanus* eggs hatched, there is probably a slight natural variation about this value. Lobsters with and without nemerteans had similar eye indices ($p > 0.05$); consequently, the data were combined (Table 3). The mean eye index may have been slightly underestimated due to egg shrinkage during the fixation process; furthermore, the eye indices for August 1982–83 were probably biased to lower values because some eggs hatched prior to sampling; consequently, only lobsters with less developed eggs would have been collected.

TABLE 3. Lobster egg development (eye index, μm) during July and August 1982–83.

	1982		1983	
	July	August	July	August
Mean	350	449	406	419
SE	11	11	8	10
Minimum	324	341	287	340
Maximum	470	610	561	571
N	19	37	59	60

In relation to P. homari

Prevalence of nemertean infestation remained at about 70% for 0–0.75 of eggs lost (Fig. 4). However, above 0.75 proportional egg loss, prevalence declined to 46% suggesting that egg loss was associated with nemertean loss from lobsters.

Mean density significantly increased ($p < 0.01$) from 0.40 to 4.22 nemerteans/1000 lobster eggs with increase in proportional egg loss (Fig. 4). Also, there was a significant ($p < 0.01$) correlation ($R = 0.35$, df = 577) between egg loss and density after the latter was $\log_{10}$ transformed.

Tag returns

Of the 1410 newly ovigerous lobsters tagged during July–October 1982, the total number of recaptures was 1136 (includes multiple recaptures between months but not within a month) between August 1982 and August 1983 (Fig. 5). Of the 208 individual lobsters recaptured between April and July 1983, 6.3% were no longer ovigerous. The percentage of females that had lost all their eggs was low (0–1.2%) prior to

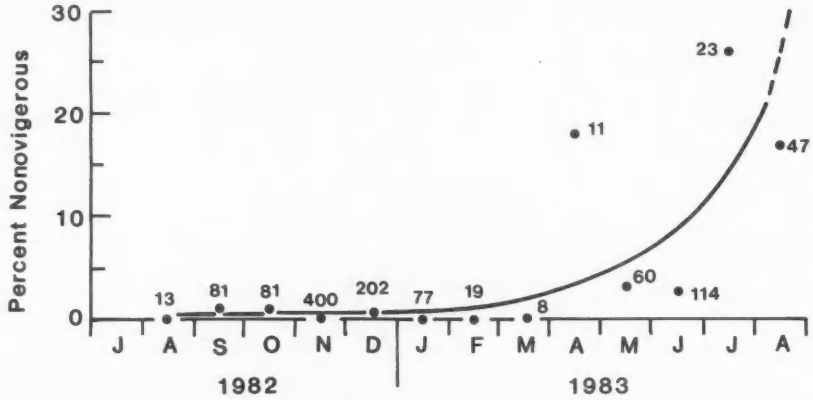

FIG. 5. Percentage of recaptured tagged female American lobsters that were no longer carrying eggs during the egg incubation period for eggs extruded July–September 1982. Numbers next to points are the total numbers of individual lobsters recaptured per month; multiple recaptures of a lobster in one month were treated as only one recapture per month, i.e. multiple recaptures (i.e. >1) were excluded within each month but not between months. The line was eye-fitted after calculating 3-mo running averages.

TABLE 4. Relationship between nemertean density and egg loss in tagged ovigerous lobsters sampled at release (second pair of abdominal pleopods) and at recapture (third pair of abdominal pleopods).

CL (mm)	Release–recapture dates	Eye index (μm)	Nemerteans/ 1000 lobster eggs	Proportional egg loss
114	17 Sept. 1982	0	0.62	0.02
	26 July 1983	356	0.17	0.32
151	1 Nov. 1982	0	10.88	0.46
	21 June 1983	347	2.95	0.78
131	1 Nov. 1982	0	2.83	0.34
	2 Aug. 1983	347	0.87	0.58
149	1 Nov. 1982	0	6.59	0.20
	4 Aug. 1983	285	16.25	0.66
141	24 Nov. 1982	0	9.92	0.27
	20 June 1983	327	2.67	0.76
142	18 Jan. 1983	266	0.24	0.16
	12 Apr. 1983	313	0	0.20
139	18 Jan. 1983	290	5.02	0.41
	10 Aug. 1983	424	0.19	0.67

April 1983, but increased slowly to about 20% by mid-August. The high (18.2%) value in April, compared with the two subsequent months, could be attributed to a small sample size (Fig. 5). The cause of total egg loss for these tagged females is unknown and the exact time when egg loss occurred is uncertain, since the curve in Fig. 5 indicates a cumulative relationship over time. Eye-spot indices suggest that some egg hatching occurred during July and August (Table 3); the increase in nonovigerous females during July–August 1983 could, therefore, have been the result of some females hatching all their eggs. However, if we assume that factors other than egg hatching caused total egg loss, the overall egg attrition from the lobster population (T) (including lobsters that lost part or all of their egg mass) during 1982–83 can be estimated from the following formula: $T = 1 - R(1 - P)$ where P = mean proportion of eggs lost from lobsters that lose part of their eggs and R = proportion of lobsters still ovigerous = $1 - L$, where L = proportion of lobsters losing all their eggs. The formula assumes that total and partial egg loss from individuals is independent of lobster size. Thus, for August 1983, the maximum possible egg loss (T) was 0.54, where $P = 0.42$ (Fig. 3) and $L = 0.20$ (Fig. 5); this value is probably an overestimate because all egg loss was assumed to be due to factors other than eggs hatching. In contrast, if we attempt to remove the effect of egg hatching on egg loss estimates by assuming, say $P = 0.34$ (average June–July 1983) and $L = 0.063$ (average for April–July 1983), then $T = 0.38$.

Only seven lobsters that were recaptured had second pleopod egg samples removed. Some caution should be used in interpreting these data (Table 4) since (a) the sample size was small, (b) dates and intervals between release and recapture were not consistent, and (c) most of these lobsters had unusually high densities of nemerteans at first release compared with other lobsters sampled at the equivalent sample times (Fig. 1). However, several points emerge from Table 4: (1) most lobsters had decreases in nemertean densities with increases in egg loss and

embryo development; (2) high densities of *P. homari* (>4.0 nemerteans/1000 eggs) at lobster release or during early egg development resulted in high (>0.65) egg loss; whereas (3) low densities of nemerteans (<1.0 nemerteans/1000 eggs) at early lobster egg development resulted in relatively low (<0.35) egg loss.

An additional 27 lobsters that were tagged during July–October 1982, and sampled for pleopod eggs only at recapture during July–August 1983, had a prevalence of 81.5%, mean density of 0.79 (±1.32 SE), and mean egg loss of 0.47 (±0.04 SE).

Discussion

Ovigerous lobsters at Grand Manan lost a substantial proportion of their eggs prior to hatching. Our estimates of mean proportional egg loss from *H. americanus* (0.38–0.43) were similar to that (0.36) reported for lobsters caught on the continental shelf off New England (Perkins 1971). Egg loss in marine crustacean decapods that incubate their eggs on pleopods is not uncommon; e.g. 0.5 egg loss has been found in snow crabs, *Chionoecetes opilio* (Brunel 1963). Egg mortality was as much as 0.5 for the Dungeness crab, *Cancer magister*, with high densities of the nemertean *Carcinonemertes errans* (Wickham 1979a, 1979b).

Total egg loss from the lobster population was probably underestimated slightly because some ovigerous lobsters that lose all their eggs during the incubation period become non-ovigerous (Templeman 1940a; Ennis 1984) and would be excluded from the egg samples. Although the tag recapture data indicated that few lobsters lost all their eggs before April 1983, total egg loss from individual lobsters increased only at the end of the egg incubation period (Fig. 5). Since we were unable to determine precisely what proportion of egg loss was due to egg hatching, we estimated that total egg attrition from the lobster population was between 0.38 and 0.54; the latter was probably an overestimate, since this value may have included some egg hatching.

Egg loss could not be attributed solely to infestation of the egg predator *P. homari*, since there were no significant differences in egg loss between nemertean-infested and uninfested lobsters. Other causes of egg loss in our study were not investigated. However, lobster egg loss has been attributed to secondary fouling by microbial epibionts (Miller and Fleming 1983; Harper and Talbot 1984), inadequate egg adhesion, egg infertility, and handling by fishermen (Aiken and Waddy 1980), nemerteans feeding on eggs (Waddy and Aiken 1985), and cleaning or grooming of nemertean-infested eggs by ovigerous lobsters (Aiken et al. 1985). Wickham (1980) found that accumulation of yolk and fecal material, resulting from *C. errans* feeding on crab eggs, exacerbated egg loss from *C. magister* by providing a nutritious medium for the growth of microbial epibionts.

Our study indicates that the low densities of *P. homari* found on most lobsters did not cause major egg loss to the ovigerous lobster population in the Grand Manan area during 1980–83. There was, however, a low but significant correlation that suggested a relationship between nemertean density and lobster egg loss. Also, high *P. homari* densities (>4.0 nemerteans/1000 eggs) during early egg development were associated with substantial or complete egg loss (Table 4). Despite a high prevalence (>60%) for most of the months sampled, few lobsters lost all their eggs and average egg losses ranged between 0.38 and 0.43 at the end of the three incubation periods.

Although *P. homari* can destroy lobster egg masses (Aiken et al. 1985), a number of controlling factors in the wild seem to limit the nemertean's density and full destructive potential. Lobster egg yolk is mostly available in early development, and as lobster embryos develop, the yolk material is reduced (Templeman 1940b), providing less food material for *P. homari* (Waddy and Aiken 1985). If initial nemertean densities are low, factors such as local seasonal temperatures may slow nemertean population growth rates sufficiently to allow lobster eggs to develop fully. Some of the double pleopod egg samples from the tagged lobsters indicated egg loss accompanied by reductions rather than increases in nemertean density (Table 4). The cleaning or grooming activity of ovigerous females with their chelate pereiopods was probably a contributing factor toward removing many infested eggs and nemerteans, thereby limiting nemertean densities on the lobster egg mass (Aiken et al. 1985). In addition, nemerteans may have left the egg mass in the late stages of lobster egg development when egg yolk was no longer available.

In general, nemertean densities on ovigerous lobsters were low, and densities of greater than 2 nemerteans/1000 lobster eggs were infrequent. Brattey et al. (1985) also found that the numbers of nemerteans were consistently low, even though *P. homari* reproduced directly on lobster egg masses and could produce several generations during one lobster egg incubation period. In contrast, large numbers of *Carcinonemertes* occur on some crab species (Humes 1942; Scrocco and Fabianek 1970; Kuris 1978; Roe 1979; Wickham 1979a, 1979b, 1980). *Carcinonemertes* can range as high as 100 000 nemerteans per host, *C. magister*, with a mean annual density ranging from 1.78 to 24.96/1000 crab eggs (Wickham 1979a, 1979b, 1980).

Host size was probably important in increasing total nemertean load per whole lobster (Brattey et al. 1985). Roe (1979) found that, although nemerteans do not select crab hosts on the basis of size, larger hosts have more area to maintain nemerteans. In the present study the density of nemerteans did not significantly increase with lobster size. An intraspecific density-dependent effect may have kept the average density of *P. homari* relatively constant even though a larger host may have supported a greater total number of nemerteans. Wickham (1980) found that *C. errans* fecundity declined and growth was inhibited as nemertean density within the egg clutch of *C. magister* increased. Intraspecific interference between *C. errans* may have been operating, as the decline in worm density occurred before the crab egg (food) resources were limiting (Wickham 1980).

The decrease in nemertean prevalence as the egg incubation period progressed could have been caused by nemerteans being removed through total or partial egg loss and/or grooming (Aiken et al. 1985). Prevalence can be influenced by host sex, reproductive state, size, and probably the duration of molt cycle (Brattey et al. 1985). Wickham (1980) and Wickham et al. (1984) found that *C. errans* could be transferred during the molting and copulation processes of the crab host, *C. magister*.

The widespread distribution but low intensities of *P. homari* in the Canadian maritimes (Brattey et al. 1985) suggests a long-established evolutionary relationship between the lobster and the nemertean. The absence of a planktonic larval stage in the life history of *P. homari* (Fleming and Gibson 1981; Uhazy et al. 1985) may be an adaptation allowing the nemertean to produce multiple generations during the 9- to 12-mo lobster egg incubation period. In contrast, *Carcinonemertes* spp. on crab

species (Humes 1942; Kuris 1978; Roe 1979; Wickham 1980) have a planktonic larval stage with generally one generation on a short crab egg incubation period.

The few lobsters that acquired high densities (>4) of *P. homari* during the early stages of egg incubation appeared to suffer extensive or complete egg mass destruction. The critical time for *P. homari* infestation of ovigerous lobsters is probably during the first 4–5 mo of egg incubation when there is sufficient egg yolk available and high densities of nemerteans may eventually cause severe or total egg loss. Despite the higher prevalence (>70%) of *P. homari* on ovigerous lobsters from Grand Manan, compared with other areas in the Canadian maritimes (≤63%) (Brattey et al. 1985), less than 20% of the lobsters lost all their eggs in this study. The generally low nemertean densities, especially in the first 4–5 mo of the 1982–83 egg incubation, may be considered as not causing more than 50% loss to the lobster's reproductive potential in the Grand Manan area. However, the fact remains that some lobsters can become heavily infested with *P. homari* and suffer major egg losses. The circumstances that allow high nemertean densities to occur on a few lobsters remain unresolved.

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Morphological Comparison of Two Northwest Atlantic Redfishes, *Sebastes fasciatus* and *S. mentella*, and Techniques for Their Identification

T. J. Kenchington[1]

Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, N.S. B2Y 4A2

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A knowledge of the taxonomy of the Atlantic redfishes, *Sebastes* spp., and techniques for their field identification are essential prerequisites for rational management of their fishery, but both remain poorly known. Through analysis of a set of morphological data for *Sebastes fasciatus* and *S. mentella* of the Scotian Shelf, using multivariate techniques, I examined the potential of 15 characters as field identifiers. Although the species are significantly different, they cannot be fully separated using these characters. I suggest that electrophoretic techniques are needed for precise identifications, although a rapid method for determining the species compositions of large samples, using anal fin ray counts, could be developed.

Nous connaissons encore peu de choses de la taxonomie des sébastes de l'Atlantique (*Sebastes* spp.) et des techniques permettant leur identification sur le terrain bien que ces deux domaines constituent une condition essentielle à une gestion rationnelle de leur pêche. J'ai étudié les possibilités d'utiliser 15 caractères comme facteurs d'identification sur le terrain en analysant, par techniques à variables multiples, un ensemble de données morphologiques s'appliquant aux *Sebastes fasciatus* et *S. mentella* du plateau Scotian. Ces espèces diffèrent de façon significative, mais elles ne peuvent être totalement isolées à l'aide de ces caractères. Je formule l'hypothèse que l'identification exacte de ces espèces nécessitera de faire appel aux techniques électrophorétiques, mais il pourrait être possible de mettre au point une méthode rapide pour déterminer la composition en espèces d'échantillons importants en se basant sur le dénombrement des rayons de la nageoire anale.

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The redfishes, *Sebastes* spp., of the northwest Atlantic support a major trawl fishery which, in Canadian waters, is subject to various management measures. Although there is certainly more than one species present, each of which should form discrete stocks, all members of the genus, within each small geographic area, are currently managed as one unit.

The taxonomy of *Sebastes* remains poorly known (Kenchington 1984), despite its obvious importance to stock assessments and fisheries management in general. Two or three forms have long been recognised: the "*marinus*-type" and "*mentella*-type" or "sharp-beaked" redfish, with the latter sometimes being subdivided into the "*mentella*-type" sensu stricto and the "American form" (e.g. Templeman 1959). The three morphs have increasingly been treated as species: *S. marinus* (L.), *S. mentella* Travin, and *S. fasciatus* Storer (e.g. Robins et al. 1980).[2] Recent electrophoretic studies by Payne and Ni (1982) and McGlade et al. (1983) have confirmed that the latter pair, which provide most of the Canadian catches, are indeed distinct at the specific level.

Before these species can be managed individually, separate data will have to be gathered for each one. To do so, efficient field identification techniques are essential. Certain types of data, such as ages for growth rate calculations, need precise identifications of individuals. Other types, including commercial catch statistics, require only estimates of the relative proportions of each species in a sample. It is, however, essential that these estimates can be provided quickly and simply, since large numbers of fish will have to be examined by nonspecialist technicians.

It would clearly be desirable for these identifications to be based on external morphology (since adults of *S. mentella* and *S. fasciatus* are indistinguishable in colour). Barsukov and Zakharov (1972) have examined many morphological characters in these fishes and found that several of them differed between *S. fasciatus* and *S. mentella*. However, in every case their character domains overlapped broadly. The resulting key, involving several characters and a large measure of judgement, is not suitable for either type of identification required for management purposes. Ni (1981a) and Misra and Ni (1983) have improved on these results by using multivariate techniques. Ni (1981a) recommended using a combination of anal fin ray counts plus four other external characters for identification with an internal one, the route of the extrinsic gasbladder muscle (Hallacher 1974; Litvinenko 1980b; Ni 1981b), for a final check when necessary. However, he seems to have chosen his samples, in the field, nonrandomly and partially by

[1]Present address: CSIRO Division of Fisheries Research, G.P.O. Box 1538, Hobart, Tasmania, 7001, Australia.

[2]*Sebastes marinus* (L.) is more correctly named *S. norvegicus* (Ascanius), see Fernholm and Wheeler (1983). *Sebastes fasciatus* has been divided into two subspecies by Litvinenko (1980a). All fish of this species referred to in the present paper were *S. fasciatus fasciatus*.

TABLE 1. Characters used in the analyses of morphology of *Sebastes fasicatus* and *S. mentella*.

Morphometrics	Meristics
Standard length	Dorsal fin rays
Snout − anal fin distance	Anal fin rays
Body depth	Pectoral fin rays
Caudal peduncle depth	Vertebrae
Head length	Gill rakers on upper limb of first gill arch
Snout length	Gill rakers on lower limb of first gill arch
Schnabel length	
Orbit height	
Interorbital distance	

anal fin ray count (Ni 1981b), making his data on this character unsuitable for devising a key. Misra and Ni (1983) provided an apparently effective method for identification based on discriminant function analysis of morphometric data. However, it is neither fully precise nor rapid, and therefore is not suitable for either of the required types of identification.

I recently published (Kenchington 1983) a set of morphometric and meristic data for the redfishes of the Scotian Shelf which, though not ideally suited to the purpose, can be used to test some suggested identification methods. Those data are here analyzed, in a comparison of *S. fasciatus* and *S. mentella*, in order to examine the potential value of 15, primarily external, morphological characters as field separators of these species.

Methods

Full details of the field sampling and laboratory processing which produced the data set are given in Kenchington (1983). In brief, samples of about 20 fish each were collected on a nonsystematic, casual basis during groundfish surveys. This produced representative, but not random, samples from all areas between the Laurentian and Fundian channels and from inshore waters to a depth of 340 fth (620 m) on the continental slope. Selection of particular redfish morphs was avoided, except for 30 fish collected for McGlade et al.'s (1983) electrophoretic study (10 fish with 7 or less anal fin rays, 10 with 8 such rays, and 10 with 9 or more). With the exception of these 30 fish, no reliable species identifications were available for individuals in the data set. Up to 15 morphometric, 10 meristic, and 16 other characters, including most of those suggested as discriminators of the species by previous workers, were examined in a total of 828 specimens of *Sebastes* spp. Of these, I considered (Kenchington 1983) only the 15 characters in Table 1 as being suitable for multivariate analysis. I showed that these morphometric characters approximated to a multivariate normal distribution (once the effects of size were removed), while the meristic ones were discretely distributed, skewed, and leptokurtic. Data on all nine morphometric characters were available for 802 fish, while 665 had all six meristics. Only data from these individuals are analyzed here. Because of the nonselective sampling and the comparative rarity of *S. mentella* off Nova Scotia, less than 10% of the fish were of this species. The data collection process involved destruction of the specimens and only those used in the electrophoretic study were preserved (Kenchington 1983).

All analyses used the Biomedical Computer Programs package (BMDP: Dixon 1977; Dixon et al. 1981). The morphometric and meristic characters were separately analyzed throughout because of their different distributional characteristics and because the morphometrics are size dependent whereas the meristics are not (cf. Sokal and Rohlf 1981).

TABLE 2. Provisional key used to allocate fish to nominal species.

A. Where electrophoretic data were available, individuals were identified by the mobilities of their *MDH*-3, *GAL*-1, and *SDH*-1 bands and the protocol of McGlade et al. (1983)
Fish thus identified were distinguished as "*S. fasciatus* (electro)" and "*S. mentella* (electro)"

B. Where such data were unavailable, individuals were identified by their meristic characteristics according to the following:
$\leqslant$29 vertebrae OR $\leqslant$7 anal fin rays: "*S. fasciatus* (merist)"
31 vertebrae OR $\geqslant$ 9 anal fin rays: "*S. mentella* (merist)"
30 vertebrae AND 8 anal fin rays: "unknown *Sebastes*"
No fish fell into more than one of these groups

C. The "unknown *Sebastes*" group was further subdivided by depth of capture into "shallow" (<320 m) and "deep" (>320 m) subgroups. The "shallow unknown *Sebastes*" subgroup is probably entirely *S. fasciatus*

NOTE: This key is not recommended for the identification of fish other than those used in the present analyses.

The data were initially subjected to principal components analyses (PCAs) to provide objective multidimensional presentations of the data through ordination. The PCA of morphometrics was based on the covariance matrix of logarithmic transformed data, to reduce the effects of heteroskedasticity between size-classes, improve additivity, and reduce the effects of measurement scale (Pimentel 1979; Humphries et al. 1981). The analysis of meristic data used a correlation matrix of untransformed variables, calculated using Spearman's ρ as a nonparametric measure of correlation. Such a PCA is robust to extreme deviations from normality (Daultrey 1976). Both were calculated by BMDP 4M.

In order to interpret these PCAs better, the fish were tentatively identified using the keys in Table 2 (which are not recommended for use outside the context of this paper). The meristic values in the table were derived from Barsukov and Zakharov's (1972) key and correspond to those found by Templeman (1980), Ni (1981b), and Kenchington (1983) for fish identified by the presence of subcaudal melanophores in their larvae, by the route of their extrinsic gasbladder muscles and by electrophoresis, respectively. The depth zones used to separate fish of unknown species were based on the minimum depths of occurrence of fish with 31 vertebrae or 9 anal fin rays in Ni's (1982) histograms and Kenchington's (1983) data. Of the keys in Table 2, that using electrophoretic data is precise. The one using meristic characters probably has few errors, but leaves many individuals unidentified, and the one based on depth is extremely tentative.

The above analyses produced results seemingly opposed to those of Misra and Ni (1983), which were based on discriminant function analysis (DFA). This technique requires a priori identification of individuals and so can be misleading in the absence of a reliable identification method. However, a DFA was performed with the morphometric data purely to permit a comparison with Misra and Ni's (1983) results.

The data included fish of a wide range of ages, and so fish size cannot be considered a useful character. Thus, before performing a DFA, it was necessary to replace the morphometric data with a set of size-independent shape measures. Following Tessier (1960) and Jolicoeur (1963), the first prin-

TABLE 3. Summary of principal components analyses of morphology of *Sebastes* spp.

A. Morphometric characters

Character	Component loadings				
Component:	1	2	3	4	5
Standard length	0.273	−0.010	0.004	−0.013	0.004
Snout − anal fin	0.270	−0.014	−0.001	−0.010	0.006
Body depth	0.285	−0.010	−0.003	−0.020	0.030
Peduncle depth	0.264	−0.005	−0.022	−0.004	0.050
Head length	0.277	−0.015	0.014	−0.009	0.002
Snout length	0.265	−0.037	−0.033	0.069	−0.017
Schnabel length	0.378	0.076	0.024	0.030	−0.002
Orbit height	0.252	−0.033	0.063	−0.010	−0.028
Interorbital	0.277	0.016	−0.053	−0.042	−0.045
Eigenvalue	0.730	0.009	0.009	0.008	0.007
Cumulative proportion of total variance explained	0.947	0.961	0.972	0.983	0.992

B. Meristic characters

Character	Component loadings					
Component:	1	2	3	4	5	6
Dorsal rays	0.673	0.020	−0.117	0.167	0.702	−0.106
Anal rays	0.762	0.082	−0.253	0.031	−0.221	0.547
Pectoral rays	0.480	0.218	0.839	−0.131	−0.031	0.030
Vertebrae	0.749	0.009	−0.203	−0.064	−0.390	−0.491
Upper rakers	−0.103	0.770	−0.210	−0.580	0.127	−0.007
Lower rakers	−0.140	0.771	0.005	0.609	−0.108	−0.051
Eigenvalue	1.856	1.242	0.866	0.758	0.723	0.555
Cumulative portion of total variance explained	0.309	0.516	0.661	0.787	0.907	1.000

cipal component of the covariance matrix of logarithmic transformed morphometric data was taken as a close approximation to an axis of "size" (cf. Kenchington 1984). The transformed characters were then regressed against this component and the residuals extracted. The latter were used as approximately size-independent data for the DFA (calculated by BMDP 7M). (Because two species were mixed in the data set, there is, at present, no technique by which a fully shape-independent size component could be calculated. Humphries et al. (1981) suggested one such approach but it requires a priori identifications and, in the present case, produced inter-"species" differences that were artifacts of group allocation.) Fish labelled "*S. fasciatus*" and "*S. mentella*", whether by the electrophoretic or meristic keys, were treated as being of known group a priori.

Results

The first principal component of the morphometric covariance matrix is a general component with approximately equal loadings by all characters (Table 3A). It explains 95% of the variance. The subsequent components are bipolar with highly variable loadings. Thus, following Pimentel's (1979) criteria, the first component appears to be an acceptable measure of fish size. However, the loadings on it are somewhat uneven, particularly that by schnabel length. Its use as a size axis therefore conceals some shape information.

Figure 1 shows the fish arranged on the first three of these principal components, which together account for 97% of the information in the morphometric data set. There is no dichotomy within these data and the range of morphometric variation of *S. mentella* is almost entirely contained within that of *S. fasciatus*. No *S. mentella* have low scores on the first principal component; that is, there were no small fish of this species in the data set.

The analysis of meristic data (Table 3B; Fig. 2) produced a first principal component which separates fish with high vertebral, dorsal fin ray, and anal fin ray counts and low numbers of gill rakers from those with the reverse. These forms are presumably *S. mentella* and *S. fasciatus*, by Barsukov and Zakharov's (1972) key. When plotted, these scores again show no clear dichotomy, but there is little overlap between the species, as identified by the key (Table 2). If the "shallow unknown *Sebastes*" subgroup is taken to be *S. fasciatus*, a minimum overlap is found using a combination of the first and third principal components; 8 of 665 fish (1.2%) lie within the overlap zone. While this is close to total separation, it must be noted that the meristic key (Table 2) used characters on which this first principal component loaded heavily.

The DFA of approximately size-independent shape measures

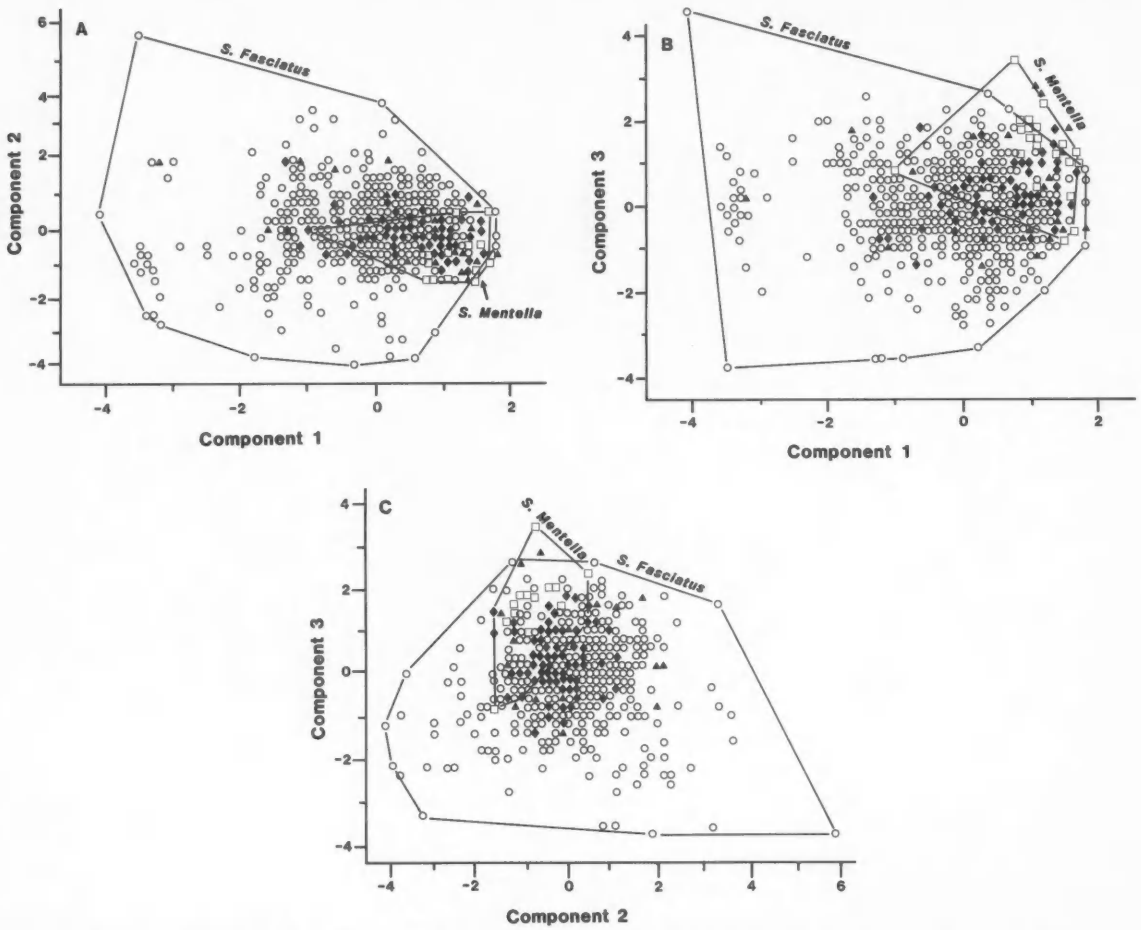

FIG. 1. Principal component scores from analysis of morphometric data, with fish identified by key in Table 2 (○, *S. fasciatus*; □, *S. mentella*; ▲, unknown *Sebastes*; ◆, groups overlapped).

is summarized in Table 4. The difference between the species centroids is very considerable ($F = 56.26$, $P \ll 0.001$) and 95% of the fish were "correctly" identified by the discriminant function. However, all of the canonical variate scores for *S. mentella* lay within the range for *S. fasciatus* (Fig. 3). Some real difference in shape will have been lost in removing the "size" effects, but the morphological overlap between the species appears to be very wide.

In summary, although the *S. fasciatus* and *S. mentella* of the Scotian Shelf have statistically very significantly different body forms, they cannot be clearly distinguished on the basis of these morphometric data. They are more distinct in their meristic characteristics, but even when using a two-dimensional combination of six characters, about 1% of the individuals remain within an overlap zone.

Discussion

These results are compromised by the inevitable lack of reliable species identifications for most individuals, by the few *S. mentella* in the data set, and by the small number of characters analyzed. However, they appear to show that the mean character states of *S. fasciatus* and *S. mentella* differ. Thus, my results are in partial agreement with Barsukov and Zakharov (1972), Ni (1981a), and Misra and Ni (1983). However, those authors' conclusion that these species are morphologically distinct is not supported. On the contrary, the PCAs clearly show that, in a range of morphometric characteristics, the two species are virtually indistinguishable. In meristic characters, there is little overlap with the present data set when the fish are given specific identifications based on the same data. Whether this is a true dichotomy or an artifact of identification is unclear.

The disagreement between the present results and those of earlier workers might be due to the deficiencies of the present data set. Certainly, a larger suite of characters might have improved separation of the species, and my conclusions can only be applied with certainty to the characters used here. However, the data set included those characters which Barsukov and Zakharov (1972) and Ni (1981a) suggested were the best meristic discriminators, so any deficiency in my character suite cannot be the sole explanation for the disagreement. Identifications based on firm data, such as electrophoretic results, might have somewhat reduced the species overlap in

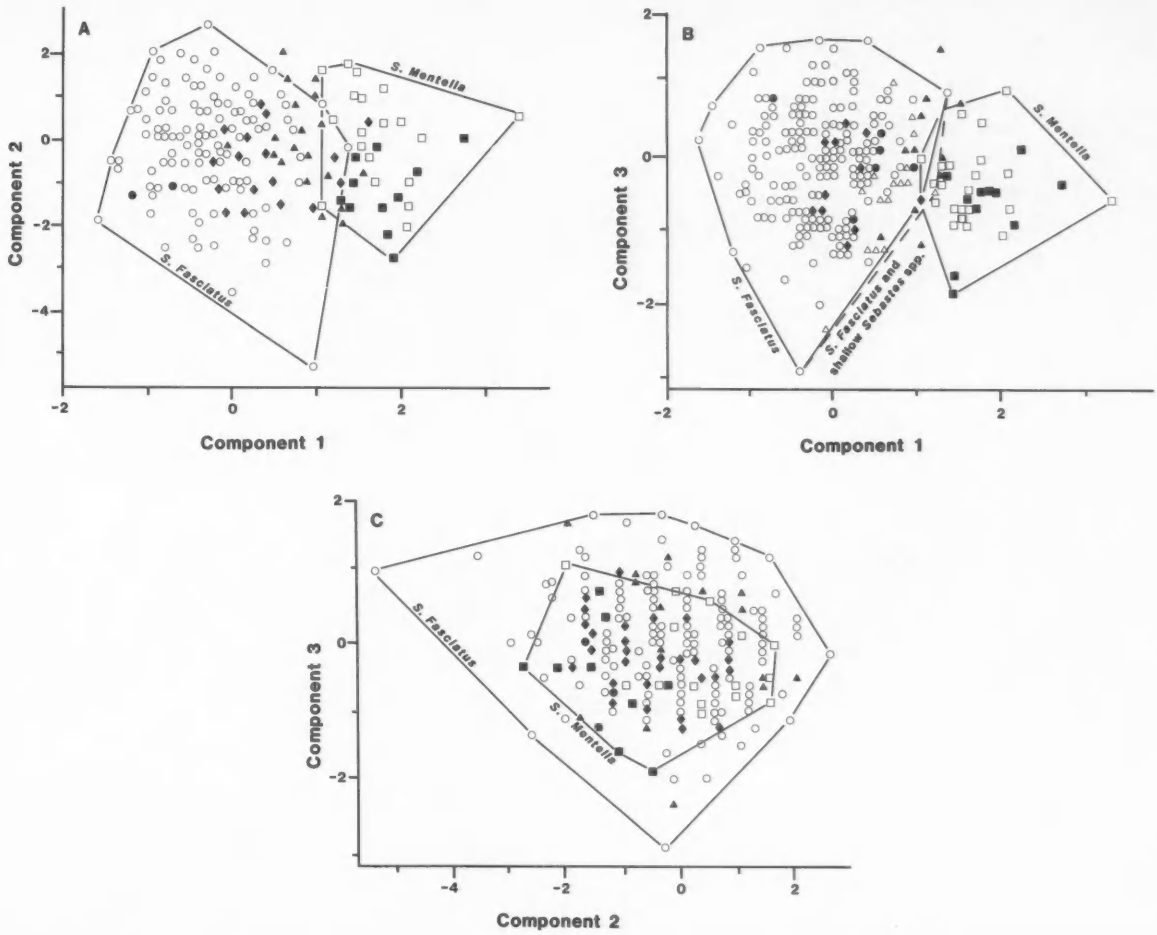

FIG. 2. Principal component scores from analysis of meristic data, with fish identified by key in Table 2 (○, *S. fasciatus* (merist); ●, *S. fasciatus* (electro); □, *S. mentella* (merist); ■, *S. mentella* (electro); ▲, unknown *Sebastes*; △, "shallow" unknown *Sebastes* subgroup (for clarity, distinguished only in Fig. 2B); ◆, groups overlapped).

morphometric characteristics, but could only have increased the one in meristics when compared with the present circular reasoning. Similarly, any increase in numbers of *S. mentella* might have produced clearer bimodality of characteristics within the data set, but could not have eliminated the present overlaps. Thus, the present and earlier works must be carefully examined for the source of the dispute.

My fish were collected from a broad area (Kenchington 1983), albeit one much smaller than either species' range. They were also, with a few exceptions, gathered without selection on the basis of morphology. Ni seems to have chosen his fish partially by anal fin ray count (Ni 1981b) and may thus have narrowed the variation of at least this character. He also took all his fish from a very limited area (less than 8 km radius; Ni 1981a, 1981b). Since *Sebastes* seem to show extreme local patchiness in both genetic (Altukhov 1974, 1981) and morphological (Kenchington 1984) characteristics, Ni (1981a) may have compared not the morphological character domains of two species, but only the more limited domains of two local forms, albeit one from each species. His dichotomy between the species in canonical variate score would then be an artifact of sample selection.

Ni's (1981a) analyses of meristic and "morphological" data used linear discriminant function analyses. These asssume homogeneity of variance–covariance matrices and, in the form which Ni (1981a) used, are unsuitable for discretely distributed data (Habbema and Hermans 1977). Yet his meristics were, of course, discrete and showed considerable interspecies differences in variance (Ni 1981a). Furthermore, the analyses included anal fin ray count, which seems to have been used in the initial selection of the specimens (Ni 1981b). Given these problems, Ni's (1981a) conclusion that *S. fasciatus* and *S. mentella* are discrete in meristic characteristics must be rejected as unsupported.

Misra and Ni (1983) analyzed morphometric data from these same specimens and so their work is subject to some of the above criticisms. However, their size-corrected DFA should be comparable with the one reported here. Both found highly significant differences between the morphometry of the species, but Misra and Ni (1983) claimed to find a minimal overlap

TABLE 4. Summary of discriminant function analysis of morphometric residuals comparing *Sebastes fasciatus* and *S. mentella*.

Step	Variable entered	Approx. *F*	df	Coefficients for canonical variable
1	Orbit height	102.47	1,730	−70.39591
2	Body depth	95.01	2,729	11.40676
3	Peduncle depth	81.75	3,728	6.25884
4	Standard length	66.71	4,727	−10.67474
5	Snout length	56.26	5,726	−2.85797
	Constant			−0.07827

F-matrix

	Unknown	*S. fasciatus*	
S. fasciatus	15.50	—	
S. mentella	13.42	56.26	df = 1,731

Classification matrix

	Percent correctly identified	Number of fish classified	
		S. fasciatus	*S. mentella*
Unknown	—	49	21
S. fasciatus	95.6	657	30
S. mentella	88.9	5	40

between them in canonical variate score whereas the analysis described above found *S. mentella* to lie entirely within the range of variation of *S. fasciatus*. However, their conclusion was based on the proportion of individuals with a posteriori identifications which disagreed with their a priori ones (or agreed, but with a probability of less than 0.05). They found 4% of their fish in this zone of uncertainty whereas for my data set, 35 of 732 fish (4.8%) lay in such a zone. Misra and Ni's (1983) criterion of overlap is unsuitable, therefore, presumably because it relies on a circularity of identification, and there is little real difference between their results and those reported here.

The present DFA involved size correction using an axis which included some shape information as "size." This will have increased the degree of overlap between the species. However, the preponderance of *S. fasciatus* in the data set will have caused the axis to be close to true size for that species, rather than lying between the species−centroids and encompassing much of the discriminating information, as might have occurred with more equal sample sizes. Thus, my DFA was not greatly affected by this source of error.

In summary, the PCAs reported here indicate a broad overlap in the measured ranges of morphometric variation of Scotian Shelf *S. fasciatus* and *S. mentella*. An examination of Misra and Ni's (1983) results gives no reason to suppose that these species are more discrete further north, and it is likely that *S. fasciatus* and *S. mentella* have broadly overlapped morphometry both on the Scotian Shelf and east of Newfoundland. I conclude that, unless some further discriminating character can be found, there is no value in attempting to develop a morphometric key for field identification of these species. A meristic approach, as proposed by Barsukov and Zakharov (1972) and Ni (1981a), is more promising. However, even when using a combination of six characters, one of which requires radiography, and with a priori and a posteriori identifications using some of the same data, the species could not be totally separated. If field radiography facilities were available for vertebral counts, together with a meristic key based on large samples of randomly selected fish of known species, it might be possible to achieve adequately precise identifications, though at great cost in time. However, it appears unlikely that external morphology alone will be able to provide full separation of *S. fasciatus* and *S. mentella*.

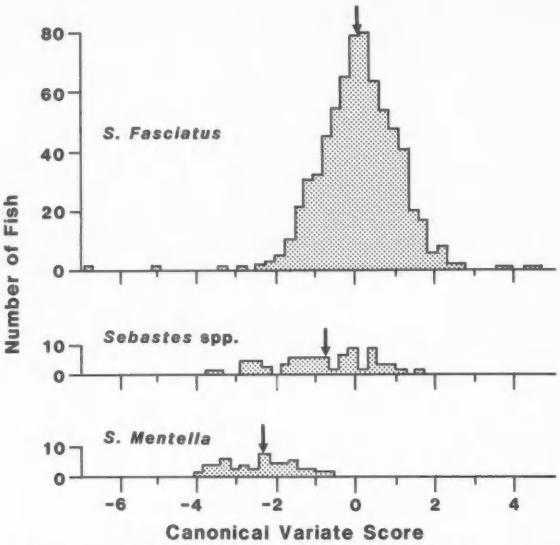

FIG. 3. Canonical variate scores from discriminant function analysis of morphometric data (origins of the three groups offset to display them clearly; centroids marked with arrows).

Where individual fish must be precisely identified, as with those collected for ageing or the development of meristic keys, it will be necessary to use a more complex technique such as the electrophoretic protocol of McGlade et al. (1983) or the routing of the extrinsic gasbladder muscle (Hallacher 1974; Litvinenko 1980b; Ni 1981b). Hallacher's (1974) dissection requires about 10 min per fish and so is too slow for routine field use. My attempts to develop a faster determination of the gasbladder muscle route (Kenchington 1983) were unsuccessful. Thus, the electrophoretic approach appears best suited to the development of a rapid and convenient identification method.

When only an estimate of the relative frequency of the two species in a sample is required, such as when preparing commercial catch statistics, it might best be obtained using anal fin ray count. This seems to be the single best external morphological separator of the species (Barsukov and Zakharov 1972) and can be counted rapidly. A large proportion of individuals of each species have eight anal rays (Barsukov and Zakharov 1972), but if the frequency of various ray counts in each species were known, their relative abundance in a large sample could be estimated by comparing the ratio of seven-rayed (*S. fasciatus*) to nine-rayed (*S. mentella*) fish. This technique might usefully be supplemented by depth of capture and fish length information. However, before such an identification method could be applied, the appropriate ray counts, depths, and length ranges for each species in each area would have to be determined using specimens identified by the electrophoretic technique.

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Empirical Prediction of Crustacean Zooplankton Biomass in Nutrient-Poor Canadian Shield Lakes

N. D. Yan

Ontario Ministry of the Environment, Dorset Research Centre, P.O. Box 39, Dorset, Ont. P0A 1E0

Yan, N. D. 1986. Empirical prediction of crustacean zooplankton biomass in nutrient-poor Canadian Shield lakes. Can. J. Fish. Aquat. Sci. 43: 788–796.

A comparison of the predictive power of nine existing empirical zooplankton biomass models indicated that lake water phosphorus concentration may be a better predictor of zooplankton biomass in Canadian Shield lakes than phytoplankton biomass, chlorophyll a, midsummer epilimnetic temperature, mean surface water temperature, mean depth, and Carlson's trophic state index. To develop models specifically applicable to nutrient-poor Canadian Shield lakes, a variety of morphometric, chemical, and planktonic parameters were assessed for three consecutive years from 16 Canadian Shield lakes in south-central Ontario. Total nitrogen was the best univariate predictor of zooplankton biomass for data averaged over single ice-free seasons, but total phosphorus was the best predictor when data were averaged over the entire study period. Consideration of pH and maximum depth improved certain models. Total phosphorus is clearly a good predictor of (long-term) average zooplankton biomass in nutrient-poor lakes as it is in lakes exhibiting a wide range in trophic state.

La comparaison de la valeur prévisionnelle de neuf modèles empiriques actuels relatifs à la biomasse zooplanctonique a indiqué que la concentration de phosphore dans l'eau des lacs pourrait être un meilleur indicateur de la biomasse zooplanctonique des lacs du Bouclier canadien que la biomasse phytoplanctonique, la concentration de chlorophylle *a*, la température de l'épilimnion au milieu de l'été, la température moyenne de la surface de l'eau, la profondeur moyenne et l'indice d'état trophique de Carlson. Pour élaborer des modèles spécifiquement applicables aux lacs pauvres en éléments nutritifs du Bouclier canadien, on a évalué pendant trois années consécutives divers paramètres morphométriques, chimiques et planctoniques relatifs à 16 lacs du Bouclier, dans la partie sud-centrale de l'Ontario. L'azote total était la meilleure variable aléatoire unique dans la prévision de la biomasse zooplanctonique, lorsqu'on prenait la moyenne des valeurs acquises pendant des périodes entières d'eau libre de glace; mais si l'on prenait la moyenne pour toute la durée de l'étude, le phosphore total était alors le meilleur élément prévisionnel. En tenant compte du pH et de la profondeur maximale, on est parvenu à améliorer certains modèles. De toute évidence, le phosphore total est un bon élément prévisionnel (à long terme) de la biomasse zooplanctonique moyenne dans les lacs pauvres en éléments nutritifs, comme dans les lacs caractérisés par une vaste gamme d'états trophiques.

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As limnologists and fisheries biologists are interested in predicting the effects of anthropogenic activities on phytoplankton and fish standing stocks, the aquatic ecology literature contains many empirical models (sensu Rigler 1982) which may be used to predict levels of chlorophyll *a*, the usual surrogate of phytoplankton biomass, and the yield or biomass of fish communities in lakes (reviewed by Ryder et al. 1974; Nicholls and Dillon 1978; Hanson and Leggett 1982; Smith 1982). Various investigators have suggested that the predictability of both chlorophyll levels (Brocksen et al. 1973; Shapiro 1979; Smith 1982; Zimmerman et al. 1983; Prepas and Vickery 1984) and fish yield (Patalas and Patalas 1968; Brocksen et al. 1973; Mills and Schiavone 1982) might be improved by explicit consideration of zooplankton. This has stimulated interest in the development of empirical models useful for the prediction of zooplankton biomass, a possibility first suggested by Rawson (1953).

Variables that have been proposed as predictors of zooplankton, or in Rawson's case, of net plankton biomass, include mean depth (Rawson 1953), surface water temperature (Patalas 1975; Watson and Wilson 1978), phytoplankton biomass (McCauley and Kalff 1981), chlorophyll *a* (Rognerud and Kjellberg 1984), total phosphorus (Hanson and Peters 1984), and Carlson's trophic state index (Bays and Crisman 1983). With few exceptions (Hanson and Peters 1984), the predictive capabilities of the proposed models have not been compared. The first purpose of this report is to compare the predictive power of existing zooplankton biomass models using data from nutrient-poor Canadian Shield lakes in central Ontario, Canada. The second purpose is to determine if improved empirical models of herbivorous or total crustacean zooplankton biomass can be developed for nutrient-poor Canadian Shield lakes in Ontario using simple morphometric, chemical, or phytoplanktonic data from the lakes.

Description of Study Lakes

Zooplankton samples were collected in 16 Canadian Shield lakes in south-central Ontario from 1977 to 1979. The watersheds of the lakes are virtually continuously forested with trees characteristic of the Great Lakes – St. Lawrence Forest Region. Human use of the lakes is entirely recreational and varies from 0 to 100 man-years per lake per year.

Selected geographic and morphometric data for the study lakes are presented in Table 1. Average total phosphorus (TP) concentration ranged from 5 to 18 $mg \cdot m^{-3}$ among the study lakes, and Secchi transparency ranged from 2.5 to 7.7 m mainly because of differences in colour among the lakes (P. J. Dillon et al., unpubl. data). The molar ratio of average total nitrogen (TN) to average TP concentration exceeded 55 for all

TABLE 1. Selected geographical and morphometric data for the study lakes.

Lake	Latitude (N)	Longitude (W)	A_o (ha)	$\bar{z}$ (m)
A Lakes				
Blue Chalk	45°12′	78°56′	49.4	8.5
Chub	45°13′	78°59′	32.2	8.9
Dickie	45°09′	79°05′	93.2	5.0
Harp	45°23′	79°08′	66.9	12.4
Jerry	45°23′	79°06′	50.1	12.4
Red Chalk (main)	45°11′	78°56′	43.9	16.7
Red Chalk (east)	45°11′	78°56′	13.0	5.7
B Lakes				
Basshaunt	45°07′	78°28′	47.3	7.7
Bigwind	45°03′	79°03′	111.0	10.7
Buck	45°23′	79°00′	40.3	10.9
Crosson	45°05′	79°02′	56.8	8.4
Glen	45°08′	78°30′	16.3	7.2
Gullfeather	45°06′	79°01′	65.9	4.8
Little Clear	45°24′	79°00′	10.9	8.1
Solitaire	45°22′	79°00′	124.0	13.3
Walker	45°24′	79°05′	68.2	6.2

the lakes, indicating that phosphorus was the element limiting phytoplankton yield (Schindler 1977). Details of the composition of the phytoplankton and zooplankton communities of the lakes are provided elsewhere (Nakamoto et al. 1983; Hitchin and Yan 1983).

The pH of the lakes ranged from 5.5 to 7.3. Although precipitation is very acidic in the area (Dillon et al. 1978) and ephemeral reductions in surface water pH associated with snowmelt have been observed (Jeffries et al. 1979), the higher colour of the four most acidic lakes (Chub, Dickie, Crosson, Gullfeather) indicates that their greater acidity (average pH < 6.0) is at least in part attributable to organic acids. The pH of the remaining lakes ranged from 6.2 to 7.3 (P. J. Dillon, Ontario Ministry of the Environment, P.O. Box 39, Dorset, Ont., unpubl. data).

Methods

Sample Collection and Analysis

The A and B lakes (Table 1) were visited weekly and monthly, respectively, during the ice-free seasons of 1977–79. Water samples were collected and analysed using methods detailed by Scheider et al. (1983) and Ontario Ministry of the Environment (1981), respectively. Chlorophyll *a* and phytoplankton biomass were determined from volume-weighted composite samples taken through a depth corresponding to twice the Secchi transparency. Other chemical determinations were performed on volume-weighted composites of the entire water column. Large zooplankton were excluded from all chemical samples by filtration through 243-μm mesh immediately after sample collection.

Hitchin and Yan (1983) detailed sampling and enumeration methods used for crustacean zooplankton. Briefly, all samples were collected at the deepest location in each lake, the two distinct basins of Red Chalk Lake being considered as separate lakes. In 1977, volume-weighted composites were generated from samples collected at 2- to 3-m intervals from the surface to 1 m above bottom with a 34-L Plexiglas trap fitted with 76-μm mesh (Schindler 1969). The trap was not used in 1978 and 1979. Instead, four to six vertical plankton hauls of predetermined lengths were taken at the deep station with the flowmeter portion and attached net (76-μm mesh) of a Clarke–Bumpus sampler. These hauls were then combined. The length of each haul was chosen so that its contents contributed to the final composite sample a portion that matched the proportional contribution of the sampled stratum to the lake volume. Sample volumes were determined using measured filtration efficiencies. These average about 70%. If corrected for filtration efficiency, Clarke–Bumpus hauls have the same capture efficiences for most zooplankton species as do Plexiglas traps (Langeland and Rognerud 1974; Lewis 1978).

An average of about 400 animals was enumerated in each sample. Herbivore and carnivore designations followed Sprules (1980). All nauplii were assumed to be herbivorous.

Zooplankton biomass was calculated from raw counts using average dry weights of each species (Table 2). Since the intersampling interval was more variable for zooplankton than for the chemical and phytoplanktonic parameters, average biomass for each ice-free season was generated by weighting data from each date by the length of the adjoining intersampling intervals.

Error Associated with Sampling Frequency

Because temporal variability is generally the largest source of variance in estimates of average zooplankton abundance (Evans and Sell 1983) and because the B lakes were sampled less frequently than the A lakes (Table 3), the precision and accuracy of average zooplankton biomass might be reduced for the B lakes. The difference in precision between the A and B lakes was assessed by manipulating 1977 biomass data from the seven A lakes as follows. For each lake, the number of collections in the year was first set to 23 to simplify interlake comparisons by randomly eliminating 3, 2, 4, 3, and 2 collections from Chub, Dickie, Harp, and Jerry lakes and from the main basin of Red Chalk Lake, respectively. The means of all possible combinations of subsets of sizes 1–22 of the 23 collections were then compared with the arithmetic mean using all 23 collections (the best mean). The relationship between subset size and average deviation of subset mean from best mean for each lake is shown in Fig. 1. The analyses are plotted for subsets with one to six collections only, because when subset size equalled six, subset means deviated from the best mean by $<1\%$ for each lake.

The number of samples collected during the ice-free season from the B lakes varied from three to nine (Table 3). Actual temporal variability in zooplankton biomass is probably similar in the A and B lakes, since, with the possible exception of Glen Lake, the lakes are chemically and morphometrically similar and have similar plankton assemblages. Therefore, Fig. 1 indicates that, in relation to the A lakes, the precision of mean zooplankton biomass estimates in the B lakes was probably reduced by $<10\%$ for Gullfeather Lake in 1977 ($n = 3$) and by $<5\%$ for the remaining 24 estimates of mean biomass. The A and B lake data are therefore combined in this report.

Error Associated with Patchy Zooplankton Distribution

All samples were collected at a single midlake station. As the spatial distribution of zooplankton in small Shield lakes in Ontario is influenced by the wind (Langford and Jermolajev 1966), average zooplankton biomass assessed at a single location might not accurately reflect the actual average in the lake. To examine this potential error, we collected vertical metered seston hauls in triplicate from 15 m (the approximate euphotic

TABLE 2. Dry weights ($\mu g \cdot animal^{-1}$) of common crustacean zooplankton of the study lakes.

Cladocera	Weight[a]	Copepoda	Weight[a]
Bosmina longirostris	0.54	Nauplius	0.11
Chydorus sphaericus	0.90	Calanoid copepodid	0.87
Daphnia dubia	4.50	*Diaptomus minutus*	2.24
Daphnia galeata mendotae	8.76	*Diaptomus oregonensis*	3.55
Daphnia retrocurva	3.14	*Diaptomus sicilis*	13.70
Diaphanosoma sp.	1.89	Cyclopoid copepodid	1.50
Holopedium gibberum	10.94	*Cyclops bicuspidatus thomasi*	3.24
Sida crystallina	12.25	*Cyclops scutifer*	6.42
		Mesocyclops edax	6.46
		Tropocyclops prasinus mexicanus	0.47

[a]To determine weights, 50–300 animals (depending on their size) were chosen to equally represent all size-classes observed in the year. These were removed from samples, rinsed four times in distilled water to remove adhering preservative, placed on preweighted coverslips, dried to constant weight at 80°C, and weighed. Weights of rare species (none of the above) were taken from a variety of sources (Hitchin and Yan 1983).

TABLE 3. Average total crustacean (B_z) and herbivorous crustacean (B_h) zooplankton biomass (mg dry weight $\cdot m^{-3}$) in the study lakes from 1977 to 1979. The 3-yr mean and numbers of collections per year (n) are indicated.

	1977			1978			1979			3-yr mean	
Lake	B_z	B_h	n	B_z	B_h	n	B_z	B_h	n	B_z	B_h
A Lakes											
Blue Chalk	44.7	36.3	23	56.0	39.4	20	69.9	51.5	21	56.9	42.4
Chub	47.6	30.4	26	49.1	26.6	24	44.8	36.6	23	47.2	31.2
Dickie	88.4	30.7	25	28.3	21.4	27	43.9	27.4	22	53.5	43.1
Harp	33.9	27.1	27	39.5	27.1	21	47.1	36.1	21	40.2	30.1
Jerry	27.3	18.1	26	43.2	26.4	23	73.7	44.3	16	48.1	29.6
Red Chalk (main)	30.6	21.4	25	37.1	23.7	24	43.7	25.1	20	37.1	23.4
Red Chalk (east)	37.3	27.7	23	75.6	56.6	22	61.8	45.7	22	58.2	43.3
B Lakes											
Basshaunt	—	—	—	46.9	27.0	7	60.0	46.1	5	53.5	36.5
Bigwind	41.1	35.5	4	50.4	42.2	6	55.0	45.6	5	48.8	41.1
Buck	20.7	14.7	4	34.0	26.1	7	42.7	36.7	4	32.5	25.8
Crosson	70.3	36.4	5	74.2	62.3	6	76.2	59.4	5	73.5	52.7
Glen	—	—	—	108.7	86.8	6	99.7	88.2	4	104.2	87.5
Gullfeather	36.6	29.9	3	125.1	93.3	7	123.5	99.1	5	95.1	74.1
Little Clear	65.6	49.5	4	83.8	56.8	9	63.4	55.8	4	70.9	54.0
Solitaire	36.0	23.9	4	97.2	32.4	7	67.7	51.8	4	50.3	36.0
Walker	20.3	17.0	4	60.4	51.0	7	64.8	50.6	4	48.5	39.5

zone depth) at five widely spaced, open water stations in the main basin of Red Chalk Lake on 11 occasions in 1981. The basin has an area of 44 ha and is about 1 km in length. The resulting samples were preserved with nonsugared 4% formalin. They were subsequently rinsed to remove adhering preservative, dried to constant weight at 60°C, and weighed on a Cahn microbalance.

A one-way analysis of variance revealed significant ($P < 0.05$) differences in seston concentration among stations on 4 of the 11 sampling days (Table 4). However, the range in average concentration among the five stations for the ice-free season was very small (105–115.2 $mg \cdot m^{-3}$).[1]

[1]Seston concentrations in 1981 exceeded B_z values in 1977–79 in Red Chalk Lake (Table 3). In addition to year-to-year variability, the difference has two probable explanations. Zooplankton are concentrated in the euphotic zone which forms only about 60% of the total volume of the lake. The seston samples were taken from the euphotic zone only, the B_z values determined from whole lake composites. Secondly, the 76-μm mesh employed undoubtedly retained some large phytoplankters.

Phytoplankton biomass exhibits little spatial variability in the study lakes (N. D. Yan, unpubl. data). As the mean seston concentrations were also similar, this suggested that while the distribution of zooplankton was frequently patchy, a single station provided an accurate estimate of average biomass for the ice-free season for the A lakes. While significant differences were often detected among stations, the relatively low coefficient of variation among the stations on any given day (3–16% of the mean, Table 4) suggested that a single station was probably also adequate for estimating average biomass for the B lakes.

Correlation and Regression Analyses

The relationship of independent (predictor) variables with total crustacean (B_z) or herbivorous crustacean (B_h) zooplankton biomass was examined using linear correlation analysis and stepwise multiple linear regression (Draper and Smith 1981). Independent variables included TP, TN, total organic (TON), and inorganic (TIN) nitrogen, TN/TP, TIN/TP, Secchi depth chlorophyll a, and phytoplankton biomass (B_p) because of the

TABLE 4. Arithmetic mean of seston (>76 μm) concentration from triplicate tows from each of five stations (1–5) in Red Chalk Lake in 1981. *F* ratios from one-way analyses of variance are included. Single and double asterisks indicate significant station effects at $P = 0.05$ and 0.01, respectively. Coefficient of variation (C.V.) for stations means is also indicated.

	Seston concentration ($mg \cdot m^{-3}$)						
	1	2	3	4	5	*F* ratio	C.V.
June 9	69[a]	81	105	82	76	3.27	0.16
July 21	139	127	113	115	101	5.66**	0.12
July 28	118	106	118	111	84[b]	2.10	0.13
August 5	136	131	127	130	131	0.50	0.10
August 12	126	116	113	125	133	0.62	0.07
August 25	85	81	73	82	91	1.48	0.08
September 8	63	78	77	75	82	1.24	0.10
September 22	108	121	123	158	151	4.43*	0.16
October 5	109	107	107	102	101	1.16	0.03
October 23	129	149	165	172	—	4.46*	0.08
November 11[c]	236	245	226	221	280	13.24**	0.10
Mean	108.2	109.7	112.1	115.2	105.0		

[a]In duplicate: all other stations in triplicate.
[b]Excluded from ANOVA because of heterogeneous variance.
[c]High numbers on November 11 were probably attributable to resuspension of bottom sediments after autumnal overturn. These values were not included in the mean.

frequent use of these variables in assessments of trophic state and their frequent inclusion in empirical trophic status models. Colour and dissolved organic carbon (DOC) were included because of the observed range of values in the lakes (5–22 Hazen units and 1.9–9.5 $mg \cdot L^{-1}$, respectively, P. J. Dillon, unpubl. data). As Confer et al. (1983) felt zooplankton biomass might be reduced in Shield lakes at a very early stage of acidification, lake pH was also included. Finally, lake area (A_o), mean depth ($\bar{z}$), maximum depth (z_{max}), and volume (V) were included because of the relationship between lake morphometry and trophic status (Larkin 1964).[2]

While temperature might be a useful predictor of B_z (Patalas 1975), it was not included in the model building exercise because its range was so small in this data set. We could not reject the null hypothesis of normally distributed data for all parameters (Kolmogorov–Smirnov test of goodness of fit at $P = 0.01$); hence, the data were not transformed prior to model building.

Two data matrices were assembled. For data matrix 1, matrix elements were averages for each parameter for the ice-free season ($n = 46$ rather than 48, as Glen and Basshaunt lakes were not sampled in 1977). Matrix 2 was formed of arithmetic means of data over the 3-yr period ($n = 16$). I hoped that data matrix 2 might reduce unmeasured influences of climatological variation, eliminate effects of lags in zooplankton responses to changes in levels of any controlling variables, and perhaps improve the precision of biomass estimates for the B lakes.

Results and Discussion

Total zooplankton biomass averaged 57.4 $mg \cdot m^{-3}$ (Table 3), a typical level for small Precambrian Shield lakes (Schindler and Novén 1971). The ratio of $B_h : B_z$ averaged 0.74.

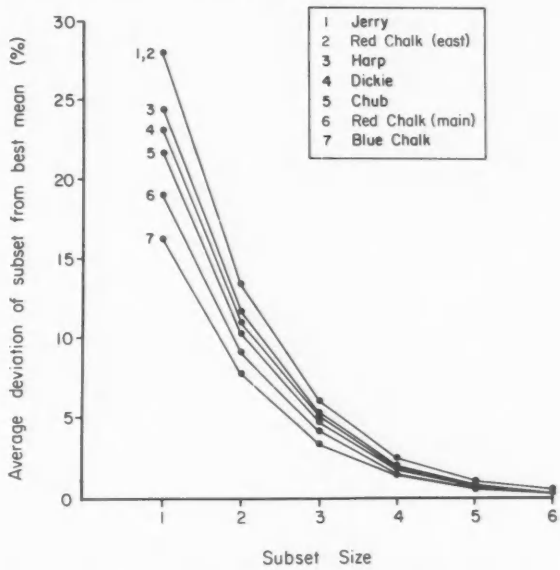

FIG. 1. Relationship between average subset size and average deviation of subset mean from the best mean ($n = 23$) for 1977 data from the A lakes.

Comparison of Existing Models

Nine existing empirical zooplankton biomass models are listed in Table 5 (Nos. 1–7, 10, 11). As Hanson and Peters (1984) used 1977 data from the A lakes (Yan and Strus 1980) in development of their models, two additional models (Nos. 8 and 9) were calculated from their data excluding data from the A lakes. The predictive capability of the models was assessed by comparison of the root mean square deviation (RMSD) of predicted from observed long-term mean (3-yr) zooplankton

[2]Raw data are available on magnetic tape on request from the Ontario Ministry of the Environment at the author's address.

TABLE 5. Compilation of existing empirical zooplankton biomass models. Zooplankton biomass (B_z) is in mg dry weight·m^{-3} except where otherwise indicated. Predictor variables include mean depth ($\bar{z}$, m), midsummer epilimnetic temperature (T, °C), mean surface water temperature ($\bar{T}$, °C), phytoplankton biomass (B_p), Carlson's chlorophyll-based trophic state index (TSIchlor), total phosphorus (TP, mg·m^{-3}), maximum depth (z_{max}, m), chlorophyll a (chlor, mg·m^{-3}) and flushing time (τ_w, yr). The range of predictor variables included in the data sets is indicated.

No.	Source	Model	r^2	n	Range
1[a]	Rawson 1953	$B_z = 3765/\bar{z}^{1.5337} + 8.0$	—	20	7.6–249
2[b]	Patalas 1975	$B_z = 0.03e^{0.217T}$	0.88	14	4.0–23.5
3	Watson and Wilson 1978	$\log B_z = 0.059\bar{T} + 0.432$	0.71	90	5–15
4[c]	McCauley and Kalff 1981	$\log B_z = 0.719 \log B_p + 1.0105$	0.72	17	0.5–40
5[d]	Bays and Crisman 1983	$\ln (B_z + 1) = 0.048\text{TSIchlor} + 2.003$	0.66	39	33–77
6	Hanson and Peters 1984	$\log B_z = 0.907 \log \text{TP} + 0.756$	0.72	49	4–200
7		$\log B_z = 0.979 \log \text{TP} - 0.158 \log z_{max} + 1.13$	0.75	49	4–200, 1.8–397
8	From Hanson and Peters 1984	$B_z = 3.75\text{TP} + 29.8$	0.57	42	4–200
9	excluding A lake data	$\log B_z = 0.94 \log \text{TP} + 0.701$	0.71	42	4–200
10	Rognerud and Kjellberg 1984	$B_z = 18\text{chlor} + 0.65$	0.62	28	0.8–4.4
11		$B_z = 8.55\text{chlor} + 6.6\bar{T} + 4.80\tau_w - 71.5$	0.75	25	—[e]

[a] B_z in kg dry weight·ha^{-1} of net plankton.
[b] B_z in mg wet weight·L^{-1}.
[c] B_z and B_p in mg wet weight·m^{-3}.
[d] B_z in μg C·L^{-1}. TSIchlor = 10[6 − (2.04 − 0.68 ln chlor)/(ln 2)], from Carlson (1977).
[e] Ranges unspecified but similar to No. 10 for chlor and 0.04–7.0 yr for τ_w.

TABLE 6. Comparison of the predictive power of existing empirical zooplankton biomass models (in Table 5) for mean (3-yr) crustacean zooplankton biomass in the A and B lakes. For each model the predicted mean biomass (Pred) and root mean square deviation (RMSD) of predicted from observed values are indicated. Both are in mg dry weight·m^{-3}. Values of predictor variables are available from the author on request.

No.	Source	Pred	RSMD
1[a]	Rawson 1953	24.1	38.8
2[b]	Patalas 1975	451.0	401.0
3	Watson and Wilson 1978	31.2	31.9
4[c]	McCauley and Kalff 1981	119.4	70.5
5[d]	Bays and Crisman 1983	110.2	57.5
6	Hanson and Peters' (1984) TP model	44.4	17.5
7	Hanson and Peters, (1984) TP + z_{max} model	76.0	26.3
8	Modified Hanson and Peters 1984: Linear	66.0	14.6
9	Log	42.2	19.2
10	Rognerud and Kjellberg 1984: Univariate	49.4	24.1
11	Multivariate	81.2	32.7

[a] B_z in kg dry weight·ha^{-1} converted to mg dry weight·m^{-3} by division by $0.1\bar{z}$.
[b] B_z in mg wet weight·L^{-1} converted to dry weight assuming a dry to wet weight ratio of 0.12 (McCauley and Kalff 1981).
[c] B_z in mg wet weight·m^{-3} converted to dry weight assuming a dry to wet weight ratio of 0.12.
[d] B_z in μg C·L^{-1} converted to mg dry weight·m^{-3} assuming the carbon content of softwater planktonic Crustacea is 45% of dry weight (Makarewicz and Likens 1979).

biomass in the A and B lakes (Table 6).

The earliest empirical zooplankton biomass model was developed by Rawson (1953), who showed that the average standing crop of net plankton (kilograms per hectare) in 20 lakes in Wisconsin and western Canada was inversely related to mean depth. Rawson's relationship provided low predictions of biomass for all but one of the 16 lakes. The RMSD of predicted from observed values was 39 mg·m^{-3}. Twelve of Rawson's 20 lakes had mean depths greater than all the A and B lakes; hence, the poor performance of his model is not surprising. For the remaining eight lakes in his study, mean depth was actually not correlated with net plankton biomass ($r = 0.23$, $P > 0.10$).

Patalas (1975) reported that the midsummer mean epilimnetic temperature of 14 large North American lakes distributed over a wide latitudinal gradient varied from 4.0 to 23.5°C and was a good predictor of zooplankton biomass. Midsummer epilimnetic temperatures in all A and B lakes exceeded 20°C. In Patalas' data set the only lakes with epilimnetic temperatures above 20°C were the south basin of Lake Winnipeg and Lake Erie, both relatively nutrient-rich systems in comparison with the A and B lakes. It is therefore not surprising that zooplankton biomass predicted from Patalas' temperature–B_z relationship greatly exceeded observed values in the A and B lakes (Table 6).

Watson and Wilson (1978) developed a relationship between average temperature of the surface waters (upper 10 m) of Lake Superior and instantaneous zooplankton biomass. Using mean surface water (1 m) temperature for the ice-free season as the independent variable, this model was a better predictor of B_z in the A and B lakes than was Patalas' midsummer epilimnetic temperature–B_z model. The RMSD of predicted from observed values was 31.9 mg·m^{-3}. Nevertheless, all predicted values were too low. This is not too surprising given the very nutrient poor status of Lake Superior.

McCauley and Kalff (1981) developed a relationship between phytoplankton and crustacean zooplankton biomass from published data. Assuming the zooplankton dry to wet weight ratio they used (0.12), their model (No. 4 in Table 5) overestimated B_z for all test lakes. The RMSD of predicted from observed values was 70.5 mg·m^{-3}. The poor performance of this model is consistent with the poor correlation of B_z with phytoplankton biomass for the A and B lakes (to be discussed).

Bays and Crisman (1983) developed a relationship between Carlson's chlorophyll-based trophic state index (Carlson 1977) and the sum of ciliate, rotifer, and crustacean zooplankton biomass for 39 lakes in Florida (Table 5). The average predicted biomass using this model was about double the measured mean in the study lakes (Table 6). The discrepancy is not attributable

TABLE 7. Pearson's product moment correlation coefficients between all independent variables in matrices 1 and 2 and B_z and B_h. Significance at $P = 0.05$ and 0.01 are indicated by single and double asterisks, respectively. Variable dimensions are indicated.

	Matrix 1 ($n = 46$)		Matrix 2 ($n = 16$)	
Variable[a]	B_z	B_h	B_z	B_h
TP ($mg \cdot m^{-3}$)	0.47**	0.50**	0.80**	0.80**
TON ($mg \cdot m^{-3}$)	0.47**	0.48**	0.52*	0.54*
TIN ($mg \cdot m^{-3}$)	0.58**	0.54**	0.70**	0.66**
TN ($mg \cdot m^{-3}$)	0.63**	0.61**	0.75**	0.73**
TN/TP	−0.04	−0.08	−0.54*	−0.55*
TIN/TP	0.17	0.11	−0.05	−0.11
Secchi (m)	−0.32*	−0.29*	−0.30	−0.26
Chlor *a* ($mg \cdot m^{-3}$)	0.24	0.26	0.28	0.31
B_p ($mg \cdot L^{-1}$)	0.14	0.16	0.38	0.40
pH	0.07	0.13	0.29	0.35
Colour (Hazen units)	0.30*	0.28	0.40	0.33
DOC ($mg \cdot L^{-1}$)	−0.11	−0.07	0.30	0.25
A_o (ha)	−0.16	−0.12	−0.26	−0.21
$\bar{z}$ (m)	−0.44**	−0.47**	−0.57*	−0.60*
z_{max} (m)	−0.48*	−0.52**	−0.65**	−0.69**
V ($m^3 \times 10^5$)	−0.30*	−0.29*	−0.42	−0.40

[a]TP, total phosphorus; TON, total organic nitrogen; TIN, total inorganic nitrogen; TN, total nitrogen; Secchi, Secchi transparency; B_p, phytoplankton biomass; DOC, dissolved organic carbon; A_o, lake area; $\bar{z}$, mean depth; z_{max}, maximum depth; V, lake volume.

TABLE 8. Regression equations with total crustacean (B_z, $mg \cdot m^{-3}$) or herbivorous crustacean (B_h, $mg \cdot m^{-3}$) zooplankton biomass as dependent variables. r_1^2 and r_2^2 are variance attributable to the first independent variable and both independent variables, respectively. The decision criterion for inclusion of parameters in regression models was an F ratio-to-include <0.05. For matrices 1 and 2, $n = 46$ and 16, respectively.

Matrix	Regression equations	r_1^2	r_2^2	SE	P[a]
1	$B_z = 25.16 + 0.15TN - 0.86z_{max}$	0.41	0.49	18.01	<0.001
	$B_h = 23.47 + 0.11TN - 0.87z_{max}$	0.47	0.48	15.29	<0.001
2	$B_z = 14.32 + 4.46TP$	0.63	—	12.35	<0.001
	$B_h = 3.94TP + 14.33pH - 84.37$	0.64	0.77	8.86	<0.001

[a]F − test.

to the exclusion of microzooplankton in this study. In Blue Chalk and Crosson lakes, two of the test lakes, Gates (1984) reported that ciliates formed <10% of the total crustacean zooplankton biomass. Rotifers form <5% of the total biomass in the A lakes (Yan and Geiling 1985). Perhaps, microzooplankton are much more important in lakes in Florida (Beaver and Crisman 1982; Bays and Crisman 1983).

Hanson and Peters (1984) assembled published data from 49 lakes with a range in TP of 3−200 $mg \cdot m^{-3}$. They concluded that TP was a better predictor of zooplankton biomass than were levels of chlorophyll or phytoplankton biomass. They also indicated that predictability of B_z was improved by inclusion of z_{max} in the model. The performance of Hanson and Peters' univariate and bivariate models (Nos. 6 and 7 in Table 5) cannot be directly compared with the other models, as 1977 data from the A lakes were taken from Yan and Strus (1980) and used in model development. However, elimination of the A lake data from their data set does not substantially alter the predictive capability of their log-transformed TP−B_z model. The RMSD of predicted from observed values increased only from 17.5 $mg \cdot m^{-3}$ for model No. 6 to 19.2 $mg \cdot m^{-3}$ for model No. 9 in Table 6.

A linear model of B_z on TP was developed after eliminating A lake data from Hanson and Peters' data set. This model (No. 8) had the lowest RMSD of predicted from observed values of all models (14.6 $mg \cdot m^{-3}$, Table 6).

Rognerud and Kjellberg (1984) recently assembled zooplankton biomass data for varying numbers of years from 18 large ($A_o = 11-365$ km^2) Norwegian lakes near Oslo. Wright (1983) indicated that lakes in this area have not been seriously perturbed by acid precipitation. Chlorophyll was a good predictor of B_z for these lakes. With an RMSD of predicted from observed values of 24.1 $mg \cdot m^{-3}$, Rognerud and Kjellburg's chlor−B_z model (No. 10 in Table 5) was a fair predictor of B_z for the test lakes. Rognerud and Kjellberg also indicated that predictability of B_z could be improved for their lakes by including surface water temperature (mean of the ice-free season) and flushing time in the model. This model (No. 11 in Table 6) actually was a poorer predictor of B_z for the test lakes than was their univariate model.

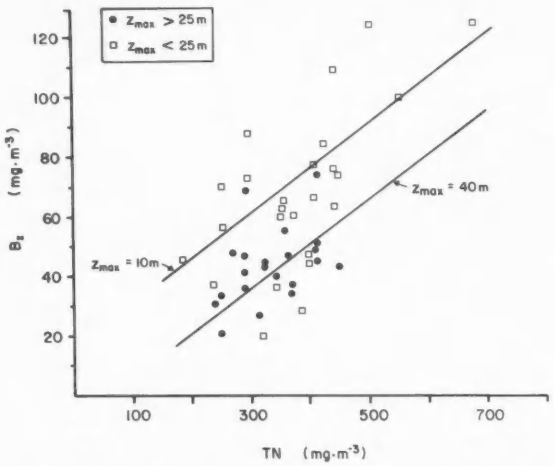

FIG. 2. Relationship between TN and B_z for data matrix 1. The lines illustrate the regression equation for z_{max} = 10 and 40 m (see first equation in Table 8).

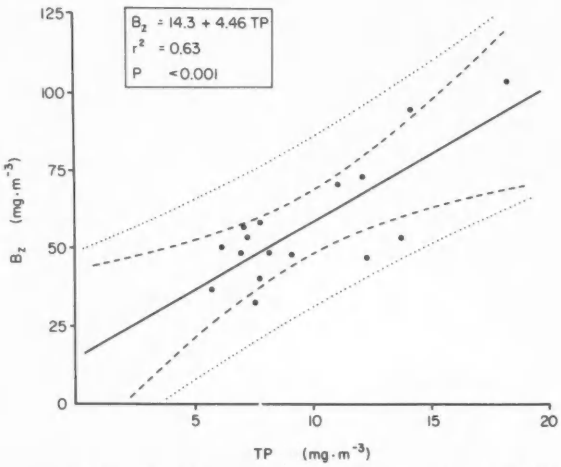

FIG. 3. Relationship between TP and B_z for data matrix 2. The 95% confidence envelopes are indicated.

Using the RMSD values as an index of model performance, the ability of these models to predict zooplankton biomass in the A and B lakes may be ranked as follows: 8 > 9 > 10 > 3 > 11 > 1 > 5 > 4 > 2 (using model numbers in Table 5). Therefore, existing models, or those calculated from existing independent data, indicate that phosphorus may be a better predictor of zooplankton biomass in nutrient-poor Shield lakes in Ontario than are mean depth, phytoplankton biomass, Carlson's trophic state index, chlorophyll, and temperature.

Correlation Analyses

Correlation coefficients of all independent variables with B_z and B_h in data matrices 1 and 2 are given in Table 7. In all cases, correlations with B_z and B_h were of similar sign and magnitude. Correlations with B_z and B_h were weak ($P > 0.05$) for TIN/TP, chlorophyll a, B_p, pH, DOC, and A_o in both data matrices. Correlations were poor in one of the matrices for

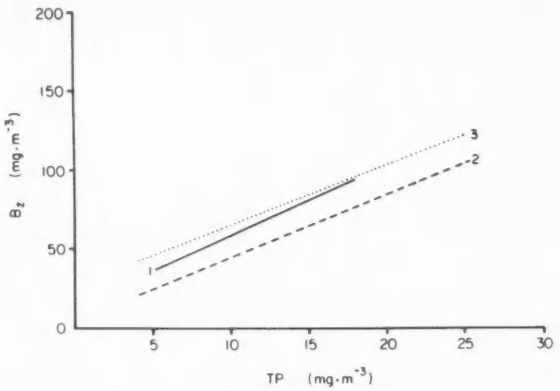

FIG. 4. Relationship between B_z and TP for three regression models: data matrix 2 in this study (1), equation 6 in Table 5 (2), and equation 8 in Table 5 (3).

TN/TP, V, Secchi depth, and colour. Significant positive correlations with B_z and B_h were observed in both matrices for TP, TON, TIN, and TN, and significant negative correlations were observed for $\bar{z}$ and z_{max}.

Over wide trophic gradients, significant positive correlations have been reported between zooplankton biomass and phytoplankton biomass (McCauley and Kalff 1981) and between zooplankton biomass and levels of TP, the latter being stronger (Hanson and Peters 1984). These correlations are to be anticipated, as, other things being equal, large differences in nutrient status among lakes should be manifest in measurable differences in standing stocks of communities at all trophic levels (Brocksen et al. 1973). For the small range in trophic status of the A and B lakes, positive correlations between zooplankton and phytoplankton biomass were not observed, while significant nutrient-zooplankton biomass correlations were observed. Two factors may underlie this result.

Firstly, phytoplankton are not the only food source for herbivorous zooplankton. Gliwicz (1969), for example, estimated that algae comprised only 50% of the diet of herbivorous zooplankton of an oligotrophic lake in Poland; bacteria and trypton formed the remainder. As about two thirds of the TP in oligotrophic lakes is particulate (Rigler 1964), TP may be a better correlate of total grazable material (algae, bacteria, and trypton) than is phytoplankton biomass. Secondly, poor correlations may be the result of seasonal changes in the net effect of zooplankton on phytoplankton. When algal nutrients are abundant, zooplankton grazing tends to reduce phytoplankton biomass. However, at other times the major source of nutrients for the algae may be the grazing activities of the herbivores (Lehman 1980). At these times, zooplankton may have a net positive influence on algal community productivity (Redfield 1980). Hence, averaged data may obscure a relationship.

Regression Analyses

The first and second independent variables selected for models predicting B_z and B_h in data matrix 1 were TN and z_{max}, respectively. However, together they explained only about 50% of the variance in the dependent variables (Table 8). Differences in sampling frequency between the A and B are probably not the cause of the large amount of residual variance (Fig. 1). A second possibility is that the timestep of the integration of the data (1 yr) is too short to reflect potential causal

relations between changes in nutrient level and response of zooplankton. Smith (1969) found, for example, that the zooplankton biomass of a Canadian Shield lake increased in the year after nutrients were added, not in the same year. Yan et al. (1982) observed a delay in zooplankton response of several months after additions of nutrients to a small acidic lake. This potential source of variance is certainly much reduced in data matrix 2.

Figure 2 is a scattergram of the relationship between TN and B_z from data matrix 1. The two plotted lines illustrate the regression of B_z on TN (Table 8) for maximum depths of 10 and 40 m, a range similar to that of the study lakes. Hanson and Peters (1984) also observed that the prediction of zooplankton biomass was significantly ($P < 0.05$) improved if z_{max} was included in the model (equation 7 in Table 5). This may simply be a consequence of the nonuniform vertical distribution of zooplankton. If zooplankton are concentrated in the euphotic zone of lakes but samples are collected over all depths, then, for lakes in which maximum depth exceeds the depth of the euphotic zone, volumetric expressions of zooplankton biomass should decrease as maximum depth increases.

In data matrix 2, TP was selected as the single independent variable in the equation predicting B_z (Table 8; Fig. 3). Most crustacean zooplankton were excluded from the total nutrient analyses in this study by prefiltration of lake water through 243-μm mesh. The phosphorus content of the zooplankton averaged only 5–11% of the mass in the water (N. D. Yan, unpubl. data), a proportion similar to that observed for other oligotrophic lakes in Ontario (Prepas and Rigler 1982); hence, the strength of the TP–B_z relationship is not attributable to the size of the zooplankton phosphorus pool.

Two independent variables (TP and pH) were included in the model predicting B_h. Together they explained 77% of the variance in the herbivorous zooplankton biomass. The inclusion of pH as a second independent variable is consistent with demonstrated positive relationships between zooplankton biomass and pH in Precambrian Shield lakes (Yan and Strus 1980; Confer et al. 1983).

For lakes exhibiting a very wide range in TP (4–200 $mg \cdot m^{-3}$), Hanson and Peters (1984) observed that TP was a better predictor of zooplankton biomass than was phytoplankton biomass. The analysis of data matrix 2 indicates that this is also true for lakes with a small range in levels of phosphorus (three- to fourfold). P. J. Dillon (pers. comm.) believes that if data are of high quality, phosphorus successfully predicts chlorophyll and phytoplankton levels even in nutrient-poor lakes. This clearly also holds for zooplankton biomass.

Two models taken or calculated from Hanson and Peters are illustrated in Fig. 4. Over a range in TP similar to that of the A and B lakes, these two relationships are very similar to that produced from the regression analysis in data matrix 2. The linear regression fit to Hanson and Peters' data falls within the 95% confidence envelope about the TP–B_z relationship developed using data matrix 2, over the indicated range in TP. Hanson and Peters' power curve falls above or just below the lower 95% confidence limit about the TP–B_z equation developed in data matrix 2.

Twenty-eight of Hanson and Peters' 49 lakes had TP levels $<25\ mg \cdot m^{-3}$, an upper limit approximating that of data matrix 1. For these 28 lakes the correlation between TP and B_z in their data is of similar sign and magnitude ($r = 0.50$, $P < 0.01$) as that observed in data matrix 1 ($r = 0.47$, $P < 0.01$, Table 7). Improvements in coefficients of multiple correlation for regression models beyond these levels can apparently be obtained first by considering means of longer time series of B_z data from the same lakes, as in data matrix 2. This probably reduces variance attributable to small sample size, to lags in zooplankton response to changes in nutrient supply, and to influences of other unmeasured variables. Alternately, the fraction of the dependent variable's variance explained by TP can be increased by increasing the range in the nutrient levels of study lakes, as in Hanson and Peters (1984).

The RMSD of predicted from measured B_z data in data matrix 2 was 11.6 $mg \cdot m^{-3}$ or about 20% of the mean observed value of 57.4 $mg \cdot m^{-3}$. This represents a slight improvement over the predictive capability of the most successful literature model, No. 8 in Table 6. As is evident in Fig. 4, the models are very similar.

The comparison of existing empirical models and the consideration of regression analyses performed in this study indicate that the average level of TP is a better predictor of long-term average zooplankton biomass in relatively nutrient-poor Canadian Shield lakes than are various morphometric and chemical parameters and phytoplankton biomass. As TP concentration can be accurately predicted for such lakes without extensive field work (P. J. Dillon, pers. comm.), it should now be possible to predict average zooplankton biomass in Canadian Shield lakes with an accuracy of ±20%.

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Trophic Status of 19 Subarctic Lakes in the Yukon Territory

Ken S. Shortreed and John G. Stockner

Department of Fisheries and Oceans, Fisheries Research Branch, West Vancouver Laboratory, 4160 Marine Drive, West Vancouver, B.C. V7V 1N6

Shortreed, K. S., and J. G. Stockner. 1986. Trophic status of 19 subarctic lakes in the Yukon Territory. Can. J. Fish. Aquat. Sci. 43: 797–805.

Limnological investigations were carried out on 19 Yukon River basin lakes in the summer of 1982 and on 10 of the lakes in March of 1983. Their surface areas ranged from 1.6 to 90 km^2 and mean depths from 2.5 to 93 m. Regression analyses were carried out using various chemical and biological variables and results were compared with similar studies in other geographic areas. Based on range in total phosphorus concentrations (3.2–12.9 $\mu g \cdot L^{-1}$), average chlorophyll levels (0.62–3.76 $\mu g \cdot L^{-1}$), and average bacterioplankton numbers (7.8×10^5 to $>10^7 \cdot mL^{-1}$), most lakes were oligotrophic, several were mesotrophic, and one was close to eutrophy. Particulate concentrations of phosphorus, nitrogen, and carbon indicated that most lakes were predominantly phosphorus limited, but in a number, nitrogen was also important in limiting phytoplankton production. The picoplankter *Synechococcus* sp. was the most abundant phytoplankton species, and common zooplankters were *Cyclops scutifer*, *Daphnia* spp., and *Diaptomus pribilofensis*.

Des études limnologiques portant sur 19 lacs du bassin versant du Yukon ont été réalisées au cours de l'été 1982 et dix de ces lacs ont été réévalués en mars 1983. La surface des lacs variait de 1,6 à 90 km^2 et leur profondeur moyenne de 2,5 à 93 m. Diverses variables chimiques et biologiques ont fait l'objet d'analyses par régression et les résultats obtenus ont été comparés à ceux d'études similaires réalisées dans d'autres régions. On a trouvé, sur la base des gammes de la concentration en phosphore total (3,2 à 12,9 $\mu g \cdot L^{-1}$), de la teneur moyenne en chlorophylle (0,62 à 3,76 $\mu g \cdot L^{-1}$) et de la concentration moyenne en bactéries planctoniques ($7,8 \times 10^5$ à $>10^7$ par mL), que la plupart des lacs étaient oligotrophes, que plusieurs étaient mésotrophes et que l'un était presque eutrophe. Les concentrations de phosphore, d'azote et de carbone particulaires indiquaient que la plupart de ces lacs présentaient une limitation par le phosphore, mais chez certains, l'azote jouait aussi un rôle important dans la limitation de la production du phytoplankton. Les espèces phytoplanctoniques les plus abondantes appartenaient au genre picoplanctonique *Synechococcus* sp. et les espèces zooplanctoniques *Cyclops scutifer*, *Daphnia* spp. et *Diaptomus pribilofensis* étaient communes.

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The Yukon Territory contains hundreds of lakes of varying morphometric and physicochemical characteristics, and most contain substantial populations of a variety of fish species, including lake trout (*Salvelinus namaycush*), northern pike (*Esox lucius*), and Arctic grayling (*Thymallus arcticus*). Various recreational, commercial, and subsistence fisheries harvest the fish populations of many Yukon lakes, and in some lakes, fishing pressure is increasing. Prior to establishment and improvement of fisheries management guidelines, it was necessary to determine the trophic status of selected Yukon lakes. Although there have been several limnological investigations in the Yukon Territory (Lindsey et al. 1981; Ennis et al. 1982; Horler et al. 1983), none have measured sufficient chemical or biological variables to determine the lakes' trophic status through comparison with data from other north temperate and subarctic lakes, and through development of empirical relationships between various biological and chemical variables.

In this study we present results from investigations of 19 Yukon Territory lakes conducted in the summer of 1982 and from 10 of the 19 lakes during ice-cover in March of 1983. This study represents the first attempt to document their current trophic status and to identify key variables controlling their productivity in this important western subarctic region of Canada.

Description of Study Area

The 19 study lakes were located in the south-central and southwestern portion of the Yukon Territory and ranged from 60°11′ to 63°43′ N and 131°40′ to 139°49′ W (Table 1; Fig. 1). All lakes except Dezadeash and Sekulmun were within the large Yukon River drainage basin. The climate in this region is subarctic, with short cool summers and long cold winters, and annual average precipitation of <50 cm. Lake elevations ranged from 579 to 1128 m above sea level (Table 1).

The lakes are dimictic with protracted periods of ice-cover, usually from October–November to May–June. Lake areas varied considerably (1.6–90 km^2) and mean depths ranged from 2.5 to 93 m (Table 1). Estimated theoretical water renewal rates ranged from 1 to 22 yr. The lakes' pH ranged from 7.3 to 8.4 and total dissolved solids (TDS) content varied from 52 $mg \cdot L^{-1}$ at the highest elevation lake (Alligator) to 290 $mg \cdot L^{-1}$ in Coghlan Lake, which is situated in a region of thick volcanic ash deposit (Lindsey et al. 1981) (Table 2).

Methods

Twenty-three locations on 19 lakes were sampled monthly from June to September 1982, and 11 locations on 10 lakes were sampled during ice-cover in March 1983 (Table 2).

TABLE 1. Geographic and physical data from the study lakes.

Lake	Latitude (N)	Longitude (W)	Elevation (m)	Lake area (km^2)	Mean depth (m)[a]	Flushing rate (yr^{-1})	Epilimnion depth (m)[b]	Surface temp. (°C)[b]	Compensation depth (m)
Alligator	60°23′	135°21′	1128	6.3	5.4	0.53	iso	11.0	7.7
Big Kalzas	63°15′	134°35′	788	42	65	0.06	9.6	11.6	7.2
Claire	61°53′	135°19′	701	20	53	0.05	8.0	13.0	12.4
Coghlan	61°33′	135°29′	732	8.2	24	0.40	9.3	12.7	33.3
Dezadeash	60°28′	136°58′	701	82	4.1	0.83	iso	10.7	—
Ethel	63°22′	136°06′	764	45	31	0.05	10.5	12.3	9.3
Fox	61°14′	135°28′	765	17	29	0.19	10.4	12.0	14.4
Jojo	60°34′	136°21′	889	6.4	31	0.16	18.3	8.9	14.0
Little Atlin	60°15′	133°57′	687	38	11	0.50	12.0	13.9	15.8
Little Salmon	62°11′	134°40′	609	63	93	0.13	13.9	10.4	12.0
Mayo	63°43′	135°04′	670	90	57	0.08	10.0	10.7	7.1
Michie	60°41′	134°10′	742	3.9	15	1.67	6.3	13.7	6.5
Quiet	61°05′	133°05′	853	53	—	—	16.1	11.0	12.3
Sekulmun	61°26′	137°33′	914	50	—	—	20.7	9.6	15.6
Snafu	60°11′	133°26′	731	3.0	6.3	5.00	7.8	14.4	13.1
Taye	60°56′	136°21′	701	8.1	2.5	5.00	iso	14.4	8.8
Twin	61°42′	135°59′	609	1.6	16	10.0	9.4	14.8	9.9
Wellesley	62°21′	139°49′	579	74	24	0.06	11.1	12.5	17.2
Wolf	60°39′	131°40′	991	74	—	—	14.6	10.2	13.2

[a]From Horler et al. (1983).
[b]June–September averages ($n = 4$).

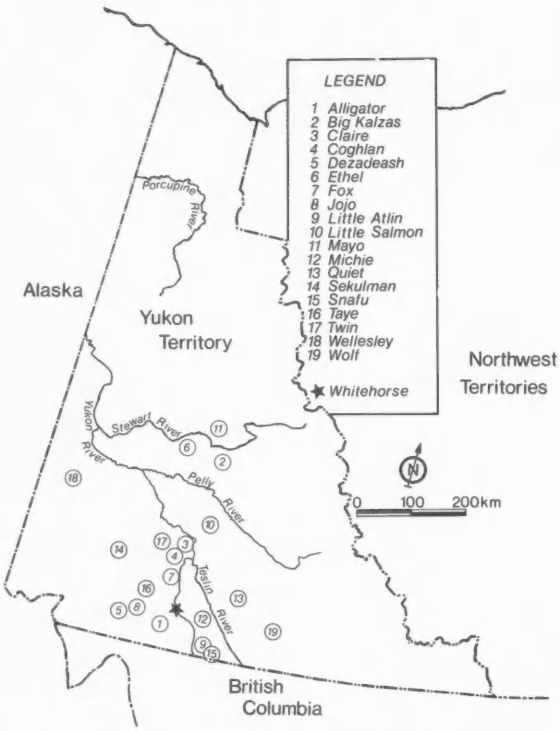

FIG. 1. Yukon Territory showing the location of the 19 study lakes.

During the open water periods we used a float-equipped Cessna 206 aircraft to reach the sampling locations, and in March of 1983 a de Havilland single-engine Otter equipped with skis.

Temperature profiles to a depth of 50 m or to bottom (whichever was less) were obtained using a Montedoro-Whitney temperature probe (model TC-5C). Buoyancy frequencies were calculated (Turner 1973) and used to calculate epilimnion depth. We used a Li-Cor light meter (model 185A) equipped with a Li-Cor underwater quantum sensor (model Li-192S) to measure photosynthetically active radiation (400–700 nm) from the surface to the compensation depth (1% of surface intensity), and calculated vertical light extinction coefficients (k). A standard 22-cm Secchi disc was used to measure water transparency.

All lake water samples were collected between 09:00 and 12:00 from two epilimnetic depths (usually 1 and 5 m) and one hypolimnetic depth in a 6-L Van Dorn bottle, rinsed with 95% ethanol. If lakes were isothermal at the time of sampling, usually only two near-surface depths were sampled. Water from each depth was placed in a clean, rinsed test tube and in polyethylene bottles. Samples were kept cold, dark, and were returned to the field laboratory within 4 h. Samples in test tubes were stored at 4°C and later analyzed for total phosphorus (TP). Water for other nutrient analyses (total dissolved nitrogen, nitrate, TDS, and soluble reactive silicon) was filtered through an ashed, washed, and rinsed 47-mm-diameter Whatman GF/F filter and placed in rinsed 125-mL glass and plastic bottles (one glass and one plastic bottle per sample). Samples were stored at 4°C in the dark and later analyzed according to the methods of Stephens and Brandstaetter (1983). At every sampling location, glass jars were filled completely with water (generally from 1 m), covered with parafilm, and transported to the field laboratory. These samples were collected to measure pH and total alkalinity according to the standard potentiometric method of APHA (1980), using a 100-mL subsample, 0.005 mol $H_2SO_4 \cdot L^{-1}$, and a Cole-Parmer Digi-Sense pH meter (model 5986-10). A 500-mL sample from each depth was filtered through an ashed and washed Whatman GF/F filter. These filters were placed in clean glass vials and later analyzed for particulate phosphorus (PP) according to the method of Stainton et al. (1977). To

TABLE 2. Average summer concentrations of epilimnetic chemical data for study lakes. Data in parentheses are from under ice in March 1983.

Lake	pH	TDS ($mg \cdot L^{-1}$)	Silicon ($mg \cdot L^{-1}$)	TN ($\mu g \cdot L^{-1}$)	PN ($\mu g \cdot L^{-1}$)	Nitrate ($\mu g\ N \cdot L^{-1}$)	PC ($\mu g \cdot L^{-1}$)	TP ($\mu g \cdot L^{-1}$)	PP ($\mu g \cdot L^{-1}$)
Alligator	7.5	52	1.99 (1.65)	333	78	<1 (13)	646	5.8 (3.3)	5.8 (0.8)
Big Kalzas	7.4	93	2.08	318	36	85	320	3.9	<2
Claire	8.2	196	4.05 (2.39)	374	65	16 (57)	424	4.6 (3.5)	3.5 (0.6)
Coghlan	8.3	290	3.88	334	48	<1	401	4.2	2.3
Dezadeash	7.5	71	1.88	281	78	<1	669	7.8	7.6
Ethel	7.3	78	0.61	277	48	5.2	351	3.2	<2
Fox	8.4	228	1.53 (1.23)	399	64	<1 (13)	397	5.6 (5.3)	2.5 (0.8)
Jojo	7.0	161	2.52 (2.11)	213	55	1.8 (15)	420	5.0 (1.7)	2.2 (0.5)
Little Atlin	8.2	139	2.70 (2.44)	382	76	1.4 (37)	545	6.1 (4.5)	3.5 (0.8)
Little Salmon	8.1	139	3.02	342	54	87	331	3.8	2.5
Mayo	7.5	97	1.69	344	47	101	395	3.2	2.3
Michie	8.3	169	4.30 (2.83)	349	80	<1	587	7.5 (9.0)	4.7 (<0.5)
Quiet	7.4	57	2.38	237	60	16	464	4.0	3.0
Sekulmun	7.2	55	3.18 (2.77)	308	42	82 (122)	320	6.9 (3.7)	2.2 (0.8)
Snafu	8.2	185	3.51	435	85	<1	609	8.2	4.8
Taye	8.2	113	3.49	822	213	<1	1763	12.9	12.7
Twin	8.3	232	3.93 (2.64)	365	72	<1 (49)	418	6.1 (4.7)	<2 (<0.5)
Wellesley	8.2	150	1.49 (1.54)	500	80	<1 (39)	576	9.2 (11.7)	6.5 (<0.5)
Wolf	7.3	81	2.60 (2.15)	253	60	2.0 (28)	490	3.5 (3.7)	2.3 (1.0)

achieve a lower detection limit for PP, a greater volume of water was filtered during the winter survey. A further 500-mL sample was filtered through a 47-mm-diameter Millipore AA filter, and a few drops of $MgCO_3$ suspension were added. Filters were dried in a desiccator and then frozen and were later analyzed for total chlorophyll using a Turner fluorometer (model 111), according to the methods of Strickland and Parsons (1972). On the July–September sampling dates only a 1-L sample from each depth was filtered through an ashed 47-mm-diameter Whatman GF/F filter. Filters were dried in a desiccator and then frozen and were later analyzed for particulate carbon (PC) and particulate nitrogen (PN) using a Perkin-Elmer CHN analyzer (model 240).

At every depth sampled a test tube rinsed with 95% ethanol was rinsed and then filled with water. In the field laboratory, 5 mL was filtered onto a 25-mm-diameter 0.2-μm Nuclepore membrane filter counter-stained with Irgalan Black. Filters were removed when just dry and placed into a 9-cm divided petrie dish lined with Whatman filter paper, air-dried at room temperature (approximately 20°C), and stored. Bacteria were counted later under epifluorescence using the acridine orange direct count (AODC) method as described by MacIsaac et al. (1981).

Picoplankton (<3 μm maximum dimension) were counted and identified using methods described by MacIsaac and Stockner (1985). Water was collected from every depth in opaque 125-mL polyethylene bottles and transported to the field laboratory where 15 mL of each sample was filtered under subdued light onto a prestained (Irgalan Black) 25-mm-diameter 0.2-μm Nuclepore membrane filter in the same manner as for bacteria biomass. Filters were then air-dried and stored at room temperature in opaque 9-cm petrie dishes. Just prior to picoplankton identification and enumeration, each filter was placed on top of a Whatman GF/F filter in a Millipore filtering unit and rehydrated with 1–2 mL of cold, filtered, distilled water for approximately 2 min. The water was then drawn through and the moist filter placed on a microscope slide, followed by a drop of Type B immersion oil, a coverslip, and then another drop of oil. Counts were made at 1250× magnification using a Zeiss compound microscope (model KLSM) equipped with epifluorescence. Approximately 20–30 random fields were counted and values were converted to numbers per cubic metre and volume (cubic millimetres per cubic metre). A minimum of 100 cells were counted per sample.

Phytoplankton samples from all depths were collected in opaque 125-mL polyethylene bottles and fixed with approximately 1 mL of Lugol's solution. Samples were later shaken and settled overnight in 27-mL settling chambers. One transect at 187.5× and one at 750× magnification were counted using a Wild M40 inverted microscope equipped with phase contrast (Utermöhl 1958). Counts were converted to numbers per cubic metre and volume (cubic millimetres per cubic metre). The equations of Strathmann (1967) were used to convert phytoplankton cell volume to cell carbon.

Zooplankton were sampled using a 100-μm mesh size SCOR-UNESCO net (mouth area = 0.25 m^2) which was hauled vertically at approximately 0.5 $m \cdot s^{-1}$ from 25 m or from near bottom (whichever was less). Samples were preserved in a borax-buffered, 4% formalin–sucrose solution (Haney and Hall 1973). In the laboratory, each sample was split in half using a Folsom plankton splitter. One half of the sample was filtered onto a preweighed Whatman GF/C filter, dried at 90°C for 24 h, and then weighed. Zooplankton biomass is expressed as milligrams dry weight per cubic metre. The other half of the sample was used for zooplankton identification and enumeration using a microcomputer-based caliper system (Sprules et al. 1981).

Results

Physics and Chemistry of Study Lakes

All lakes in our study were dimictic, although Alligator, Dezadeash, and Taye lakes (mean depths of 5.4, 4.1, and 2.5 m, respectively) were isothermal during the ice-free period. The remainder exhibited varying degrees of stratification, and average (June–September) epilimnion depths ranged from 6.3 to 20.7 m (Table 2). Average summer surface temperatures were 8.9–14.8°C, and at the first sampling date in

TABLE 3. Biological data from study lakes: average summer concentrations in the epilimnion. Data in parentheses are from under ice in March 1983.

Lake	Chl ($\mu g \cdot L^{-1}$)	PHC ($\mu g \cdot L^{-1}$)	Phytoplankton (hundreds $\cdot mL^{-1}$) Pico- (<4 μm)	Nano- (4–20 μm)	Net- (>20 μm)	Bacteria numbers (millions)	Zooplankton biomass ($mg \cdot m^{-3}$)
Alligator	1.56 (3.32)	67 (24)	775 (134)	245 (5.6)	4.2 (2.8)	2.09 (0.75)	138 (65)
Big Kalzas	1.22	26	87	77	5.9	1.05	45
Claire	1.11 (2.46)	22 (10)	357 (17)	82 (4.2)	3.2 (1.2)	1.73 (0.76)	108 (44)
Coghlan	0.64	19	217	66	2.0	1.25	65
Dezadeash	2.05	55	773	218	5.9	2.20	—
Ethel	1.83	135	129	146	11	1.06	49
Fox	0.62 (0.83)	30 (5.3)	726 (43)	92 (130)	8.8 (0.4)	1.54 (0.82)	114 (65)
Jojo	1.06 (0.56)	27 (25)	332 (467)	43 (47)	2.6 (2.2)	1.26 (0.80)	95 (70)
Little Atlin	1.55 (1.22)	43 (7)	367 (14)	115 (2.9)	4.1 (0.5)	2.16 (1.75)	182 (81)
Little Salmon	1.01	28	212	115	8.4	0.78	38
Mayo	1.09	24	166	38	8.5	1.08	28
Michie	2.17 (1.40)	52 (11)	477 (21)	82 (31)	18 (1.2)	2.33 (0.76)	88 (16)
Quiet	1.11	28	406	43	1.7	1.45	86
Sekulmun	0.81 (0.88)	22 (13)	334 (124)	106 (19)	4.2 (0.7)	1.12 (0.54)	72 (48)
Snafu	2.08	66	586	28	26	2.34	271
Taye	3.76	185	85	124	65	>10	—
Twin	1.37 (0.81)	37 (5)	425 (4.0)	52 (2.0)	2.2 (0.5)	1.95 (0.54)	56 (17)
Wellesley	1.82 (0.91)	78 (7)	731 (25)	400 (2.0)	53 (3.0)	2.46 (1.08)	202 (87)
Wolf	1.04 (1.06)	55 (12)	233 (11)	118 (2.8)	29 (15.7)	1.18 (0.89)	52 (23)

mid-June, a considerable range (4.0–14.0°C) in surface temperatures was observed. None of the lakes were excessively turbid, as average compensation depths ranged from 5.6 to 33 m. Taye and Dezadeash lakes had euphotic zones which extended to the lake bottom, and in several lakes (Claire, Coghlan, Ethel, Fox, Snafu, and Wellesley), compensation depths exceeded epilimnion depths by 1.5–3.6 times.

The high June surface temperatures suggest that spring peaks in production may have occurred in some lower elevation lakes prior to the first sampling date. In addition, differences between compensation and epilimnion depths indicate that substantial hypolimnetic production could occur in several of the lakes. Therefore, it is likely that our summer average biomass determinations are an underestimate of the true average biomass levels in some of the study lakes.

Depth of snow cover on the 10 lakes sampled in March varied from negligible on Jojo Lake (i.e. most of the ice surface free of snow) to 0.5 m on Michie lake. Ice on all lakes was clear (black) and ranged in thickness from 0.5 to 1.2 m. In March, most lakes exhibited a distinct inverse thermal stratification, with temperatures <1°C near the ice–water interface and >3°C below a depth of 15–20 m.

Chemical analyses showed considerable variation in concentrations among the 19 lakes (Table 2). Average summer silicon concentrations ranged from 0.61 to 4.30 $mg \cdot L^{-1}$, and the average of all lakes was 2.68 $mg \cdot L^{-1}$. Nitrogen concentrations varied more than any other measured chemical variable, and of the three nitrogen species determined, nitrate was the most variable. Nine lakes had average summer nitrate concentrations below the analytical detection limit of 1 $\mu g\ N \cdot L^{-1}$, and four lakes had average concentrations >80 $\mu g\ N \cdot L^{-1}$. In all lakes sampled under ice, nitrate concentrations were considerably higher than average summer concentrations. Average summer concentrations of total nitrogen (TN) ranged from a low of 237 $\mu g \cdot L^{-1}$ (Quiet Lake) to 822 $\mu g \cdot L^{-1}$ (Taye Lake) and averaged 361 $\mu g \cdot L^{-1}$ for all lakes. PN was less variable than TN and averaged 78 $\mu g \cdot L^{-1}$, or 22% of the TN in the study lakes (Table 2). PC concentrations averaged 533 $\mu g \cdot L^{-1}$ for all lakes, and were highest (1763 $\mu g \cdot L^{-1}$) in shallow, isothermal Taye Lake and lowest (320) in Big Kalzas and Sekulmun lakes. TP concentrations ranged from 3.2 to 12.9 $\mu g \cdot L^{-1}$ in summer and from 1.7 to 11.7 $\mu g \cdot L^{-1}$ in winter. Average TP concentrations for the 10 lakes sampled in winter were 5.1 (winter) and 6.0 (summer). Summer PP concentrations averaged 64% of TP (all lakes), and ranged from <2 to 12.7 $\mu g \cdot L^{-1}$ (Table 2). Winter PP concentrations were much lower, averaging only 20% of winter TP (range <0.5–1.0 $\mu g \cdot L^{-1}$).

Bacteria and Plankton in the Study Lakes

Average bacteria numbers ranged from $7.8 \times 10^5 \cdot mL^{-1}$ in Little Salmon Lake to $2.46 \times 10^6 \cdot mL^{-1}$ in Wellesley Lake, and on two of the four sampling dates, bacteria numbers in Taye Lake were too high ($>10^7 \cdot mL^{-1}$) to count by our methods. The high numbers in Taye Lake are partially attributable to the suspension of benthic bacteria from the sediment, since Taye Lake is shallow and was isothermal throughout the growing season. Although some variation in numbers occurred in each lake during the June–September sampling season, seasonal trends were not generally apparent. During the winter survey, bacteria numbers ranged from 5.4×10^5 to $1.08 \times 10^6 \cdot mL^{-1}$ and were from 28 to 81% of summer averages.

Phytoplankton biomass as chlorophyll (Chl) reached peak densities in August in most lakes. Average Chl concentrations ranged from 0.62 to 3.76 $\mu g \cdot L^{-1}$ in summer and from 0.56 to 3.32 $\mu g \cdot L^{-1}$ under ice in March 1983 (Table 3). Average Chl concentrations in the 10 lakes sampled under ice were 1.31 $\mu g \cdot L^{-1}$ in summer and 1.35 $\mu g \cdot L^{-1}$ in winter, and winter values were from 0.5 to 2.2 times those found in summer. Average phytoplankton carbon (PHC), as derived from the equations of Strathmann (1967), ranged from 22 to 185 $\mu g \cdot L^{-1}$. Winter values of PHC were much lower than average summer levels (0.09–0.59 times), except in Jojo

TABLE 4. Regression equations derived in this study with pertinent statistics. All variables were log transformed.

Y variable	*X* variable	*n*	Intercept	Slope	r^2	*p*
PP	TP	19	−0.30	1.12	0.63	<0.01
Chl	TP	19	−0.39	0.70	0.35	<0.01
Chl	TP_{sp}	10	−0.21	0.44	0.31	>0.05 (NS)
Chl	PC	19	−2.46	0.96	0.59	<0.01
Chl	PC[a]	18	−2.76	1.08	0.40	<0.01
Chl	PN	19	−1.60	0.96	0.54	<0.01
Chl	PN[a]	18	−1.55	0.93	0.32	<0.05
Chl	PP	19	−0.23	0.70	0.61	<0.01
Chl	PP[a]	18	−0.19	0.61	0.44	<0.01
PHC	PC	19	−1.56	1.19	0.45	<0.01
PHC	PC[b]	17	−2.82	1.65	0.61	<0.01
PHC	PP	19	1.23	0.80	0.39	<0.01
Bact	TP	18	5.56	0.85	0.65	<0.01
Bact	PP	18	5.86	0.66	0.70	
Bact	PC	18	2.81	1.27	0.76	<0.01
Bact	PN	18	4.01	1.22	0.76	<0.01
Bact	Chl	18	6.13	0.56	0.36	<0.01
Bact[c]	TP	30	5.60	0.91	0.80	<0.01
Bact[c]	Chl	31	6.15	0.70	0.76	<0.01
Zoopl	TP	17	0.88	1.47	0.61	<0.01

[a]Taye Lake removed.
[b]Taye and Ethel lakes removed.
[c]Our data plus those from Bird and Kalff (1984).

Lake, where winter PHC was 93% of average summer concentrations. Summer ratios of PHC:Chl ranged from 20 to 53 and averaged 34 in the same lakes that were sampled during the winter survey. Winter PHC:Chl ratios ranged from 4 to 15, with the exception of Jojo Lake, where the winter ratio was 45. Average phytoplankton numbers, which ranged from 3.78×10^4 to $1.02 \times 10^5 \cdot mL^{-1}$ in summer, were far lower in March (range 700 to $1.28 \times 10^4 \cdot mL^{-1}$), except in Jojo Lake, which had higher phytoplankton numbers in March ($5.16 \times 10^4 \cdot mL^{-1}$) than in summer ($3.78 \times 10^4 \cdot mL^{-1}$).

The phytoplankton communities in the 19 lakes had several species which were abundant in most or all of the lakes. The small (0.5−2.0 μm) cyanobacteria *Synechococcus* sp. was the most numerous species in almost all the lakes, and flagellated species such as *Chroomonas* sp., *Ochromonas* sp., and *Cryptomonas* sp. were abundant in many of the lakes. *Cyclotella* spp. (usually relatively small sizes) were the only diatoms that were common in most lakes. Large diatoms were rare except in Ethel Lake, where *Rhizosolenia* sp. was dominant. Large cyanobacteria were not dominant in terms of cell number or biomass in any of the lakes, but the nitrogen fixer *Anabaenopsis* sp. was common in Taye, Twin, and Wellesley lakes.

Zooplankton

Average summer zooplankton biomass (as dry weight) ranged from 28 $mg \cdot m^{-3}$ in Mayo Lake to 202 $mg \cdot m^{-3}$ in Wellesley Lake (Table 3). Dezadeash and Taye lakes were too shallow to obtain quantitative biomass estimates with the technique we used. Highest zooplankton biomass in almost all lakes occurred in July or August, and in most lakes, highest densities occurred in July. Zooplankton biomass under ice in March was from 18 to 74% (average = 47%) of the June−September averages. Mean size of the zooplankton community (including rotifers and nauplii) was variable among lakes,

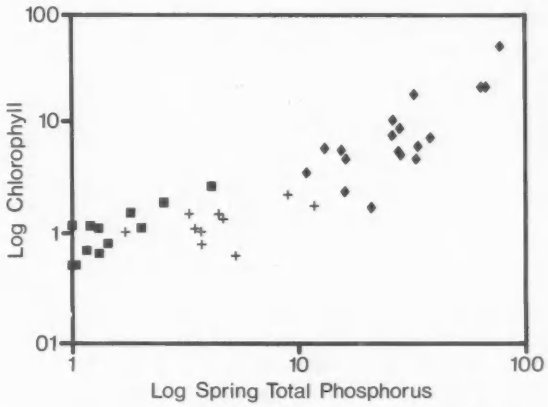

FIG. 2. Log average Chl concentration ($\mu g \cdot L^{-1}$) regressed with log TP concentration ($\mu g \cdot L^{-1}$) at spring overturn (■, monomictic British Columbia lakes (Stockner and Shortreed 1985); ◆, Prairie parkland Alberta lakes (Prepas and Trew 1983); +, this study).

and ranged from 0.39 mm in Coghlan Lake to 0.66 mm in Wellesley Lake. *Cyclops scutifer*, *Daphnia longiremis*, and *Diaptomus pribilofensis* were the most common species in the lakes, and *Daphnia* exhibited the greatest size variability of the major genera (average sizes from 0.60 mm in Snafu Lake to 1.72 mm in Wolf Lake).

Discussion

Chl and Phosphorus Relationships

The relationships between Chl:TP and between Chl:TP at spring overturn (TP_{sp}) have been well documented for many

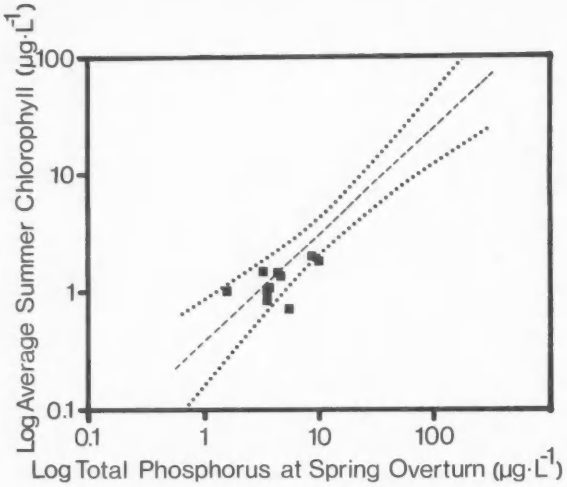

FIG. 3. Log average Chl concentration plotted with log TP concentration at spring overturn. The regression line and 95% confidence limits are from Vollenweider (1976).

dimictic and monomictic lakes in North America (Kerekes 1975; Schindler et al. 1978; Edmondson and Lehman 1981; Prepas and Trew 1983; Stockner and Shortreed 1985). A significant Chl:TP relationship existed in our Yukon study lakes, but was much weaker than those reported by other investigators (Table 4). Most of the scatter was contributed by the data points from Coghlan, Ethel, Fox, and Sekulmun lakes. Ethel Lake was the only lake in our study in which the large diatom *Rhizosolenia* sp. was dominant. The highest Chl:TP ratio (0.57) in this study occurred in Ethel Lake, while the average Chl:TP ratio for all the lakes was 0.26 (range 0.09–0.57). We have suggested earlier (Stockner and Shortreed 1985) that *Rhizosolenia* sp. has a high Chl:TP ratio, and data here support this contention. Sekulmun Lake had the lowest Chl:TP ratio of all our study, the lowest PP:TP ratio, and was an outlier in all correlations which included TP. In Sekulmun Lake, we believe a large portion of the phosphorus pool was biologically unavailable.

TP_{sp} has been widely used to predict average summer Chl concentration (Dillon and Rigler 1974; Vollenweider 1976; Prepas and Trew 1983; Stockner and Shortreed 1985), but in this study the logarithmically transformed data were not significantly correlated (Table 4). The lack of a significant relationship may be a result of the times of sampling, since Chl data were collected in the summer of 1982 and TP_{sp} data were obtained in March 1983. However, it is informative to compare these data with those from other investigations (Fig. 2). Prairie parkland lakes in Alberta (Prepas and Trew 1983) tended to have higher Chl and TP_{sp} levels than our study lakes, and TP_{sp} tended to be higher in Yukon lakes than in monomictic coastal lakes of British Columbia (Stockner and Shortreed 1985). Despite different TP_{sp} levels, Yukon and coastal British Columbia lakes tended to have similar Chl levels. We attribute this to the much greater density of zooplankton in Yukon lakes which can effectively reduce Chl levels in the absence of fish predation (Henrikson et al. 1980; Spencer and King 1984; Wright and Shapiro 1984). Vollenweider (1976) plotted Chl and TP_{sp} from lakes of widely varying trophic status, and our lakes fit well within the general pattern he reported

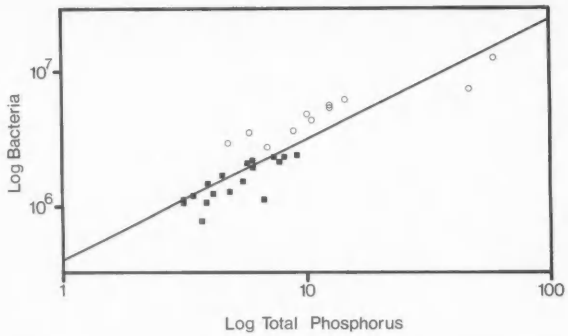

FIG. 4. Log average bacteria numbers regressed with log average TP concentration (μg·L⁻¹) (○, Quebec lakes (Bird and Kalff 1984); ■, this study).

(Fig. 3). According to Vollenweider's (1976) criteria, most of the Yukon lakes can be classified as oligotrophic, although several lie in the mesotrophic category.

PC, PN, PP, and Chl Relationships

Because PC and PN concentrations were determined from July to September only, PP, TP, and Chl averages were recalculated using only these dates in order to make valid comparisons between variables. Chl was significantly correlated with PC, PN, and PP, and although the correlations were weaker if the highest data point (Taye Lake) was removed, they remained significant (Table 4). The correlation of Chl with the various particulates showed considerable scatter and was much weaker than noted for coastal British Columbia lakes which generally have abundant populations of planktivorous fish (Stockner and Shortreed 1985). We believe that this is attributable to marked differences in zooplankton densities and attendant grazing pressure between lakes in the two regions and also to differences in nutrient deficiencies between the regions.

Healey and Hendzel (1980) utilized ratios of PP, PN, PC, and Chl to determine nutrient deficiencies in phytoplankton, and for comparative purposes we calculated the same ratios for our study lakes. On the basis of PP:PC and PN:PP ratios and Healey and Hendzel's (1980) criteria, the Yukon lakes showed slight to severe phosphorus limitation, with Alligator, Dezadeash, and Wellesley lakes showing the lowest degree of phosphorus deficiency. Ratios of PN:PC indicated that half of the lakes had no nitrogen deficiency, but the remainder were moderately nitrogen deficient. Interestingly, Big Kalzas and Mayo lakes, which showed the highest degree of nitrogen deficiency according to the PN:PC ratio, also had the highest average nitrate concentrations (85 and 101 μg NO_3–N·L^{-1}, respectively). A number of lakes had higher phosphorus and much lower nitrate concentrations than Big Kalzas or Mayo lakes, and yet had a lesser degree of nitrogen deficiency based on the PN:PC ratio. We suggest, therefore, that the physiological indicator of nitrogen deficiency (PN:PC) proposed by Healey and Hendzel (1980) may be inappropriate in some lakes, perhaps because other unidentified factors are limiting production. The Chl:C ratios found in our study lakes indicate, according to Healey and Hendzel's classification, a general nutrient deficiency more severe than that indicated by the various PP, PC, and PN ratios. The average C:N:P ratio in Yukon basin lakes was 137:18:1, lower than the ratio of 152:20:1 found in

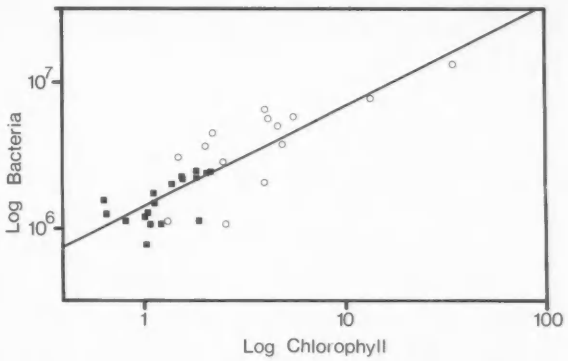

FIG. 5. Log average bacteria numbers regressed with log average Chl concentration ($\mu g \cdot L^{-1}$) (○, Quebec lakes (Bird and Kalff 1984); ■, this study).

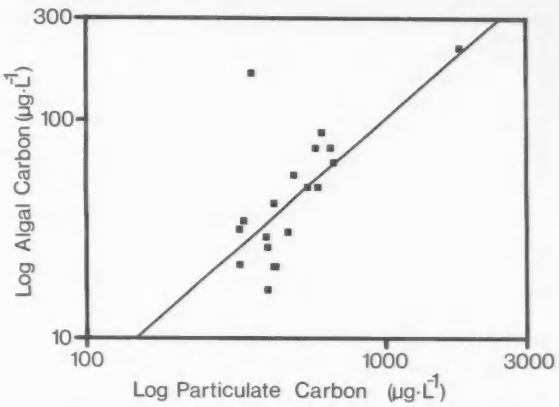

FIG. 6. Log algal carbon concentration calculated using equations from Strathmann (1967) regressed with log average PC concentration.

monomictic lakes of the British Columbia coast (Stockner and Shortreed 1985), but higher than the ratio of 108:16:1 reported for marine phytoplankton by Redfield et al. (1963). However, there was considerable variation in the C:N:P ratio in Yukon basin lakes, ranging from a low of 84:10:1 in Dezadeash Lake to 209:36:1 in Twin Lake. We conclude from the above comparisons that in most of our study lakes, as in most north temperate lakes (Schindler 1975), phosphorus was the major factor limiting phytoplankton production. However, it is probable that in several of the lakes which had only slight phosphorus deficiencies and very low nitrate concentrations that nitrogen was playing a significant role in limiting phytoplankton production.

Bacteria and Plankton

Average bacteria numbers were significantly correlated with a number of biological and chemical variables (TP, PP, PC, PN, and Chl) and in general were more highly correlated with the chemical variables than was Chl (Table 4). The largest outlier on the bacteria and TP figure is Sekulmun Lake, providing further confirmation that in lakes with large inputs of biologically unavailable phosphorus, TP concentration is a poor indicator of trophic status.

Bird and Kalff (1984) reported bacteria abundances from a number of Quebec lakes and compared those reported for a number of other areas, both marine and freshwater. We compared the data from Quebec lakes with our data, and analysis of covariance indicated that the slopes of the regression lines from the two data sets were not significantly different ($F = 1.11$, $p > 0.05$), but the intercepts were ($t = 10.4$, $p < 0.01$). We also combined the data sets and found that, although our data consisted of a narrower and generally lower range of concentrations, the combined data were highly correlated (Table 4; Fig. 4, 5). Bird and Kalff (1984) also grouped their study lakes into trophic categories using bacteria numbers and a classification derived from Chl (Forsberg and Ryding 1980). Based on their categories, 10 of our lakes were oligotrophic ($<1.7 \times 10^6$ bacteria$\cdot mL^{-1}$), 8 were mesotrophic (1.7×10^6 to $6.5 \times 10^6 \cdot mL^{-1}$), and 1 lake (Taye) was eutrophic ($>6.5 \times 10^6 \cdot mL^{-1}$).

In some of the study lakes it appears that variables commonly used to indicate trophic status (Chl, TP) are more affected than bacteria by factors which introduce considerable scatter into empirical relationships. The excellent fit of our bacteria data with data from Quebec lakes suggests that bacteria numbers may be a much better indicator of trophic status for Yukon lakes than Chl or TP, which are more affected by high zooplankton densities and, at least for one lake (Sekulmun), large inputs of unavailable phosphorus. When data from additional studies in other geographic areas are available, epilimnetic bacteria density may prove to be a superior variable for empirical equations used to estimate trophic state.

Smith and Kalff (1982, 1983) have demonstrated that smaller phytoplankton have a competitive advantage in inorganic phosphorus uptake, and as Currie and Kalff (1984a, 1984b) have noted, this suggests that when phosphorus is limiting, small phytoplankton cells should be favored. Therefore, the predominance of small phytoplankton species (picoplankton) in most of our study lakes again suggests that phosphorus is a critical factor in limiting phytoplankton production in Yukon lakes.

Although average nitrate concentrations were near or below the analytical limit of 1 $\mu g\ N \cdot L^{-1}$ in 11 of the 19 lakes, and although TP concentrations exceeded 5 $\mu g \cdot L^{-1}$ in most of those lakes, nitrogen-fixing cyanobacteria, though present, were not dominant in any lake. TN:TP ratios in the lakes ranged from 38:1 to 109:1 (mean of 63:1), much higher than the ratios which generally occur in lakes dominated by cyanobacteria (Smith 1983). This suggests that although inorganic nitrogen was in short supply, either portions of the dissolved organic nitrogen (DON) pool were available to fulfill the nitrogen requirements of the phytoplankton (Syrett 1981), or recycling by zooplankton excretion can meet necessary nitrogen quotas (Lehman 1980). Nitrogen was found to limit phytoplankton growth in subarctic lakes in both Quebec and Sweden when the lakes were fertilized with phosphorus alone (Smith et al. 1984; Persson et al. 1975). Clearly, nitrogen depletion at certain periods during the growing season also limits phytoplankton growth in Yukon lakes and influences overall lake metabolism by its control over the number of times phosphorus can be used per year (Golterman 1984).

The carbon content of the phytoplankton communities was estimated using the equations of Strathmann (1967) in an effort to determine the contribution of PHC to the total PC pool and to obtain a second independent estimate of phytoplankton biomass. PHC was strongly correlated with PC although isothermal Taye Lake had considerably higher concentrations

TABLE 5. The 19 study lakes ranked (highest to lowest) using three variables often cited as trophic state indicators. The average was obtained by ranking the mean ranks.

Lake	TP	Chl	Bacteria	Average
Alligator	9	7	7	7
Big Kalzas	15	10	18	15
Claire	12	11	9	9
Coghlan	13	18	13	16
Dezadeash	4	4	5	5
Ethel	18	5	17	14
Fox	10	19	10	13
Jojo	11	14	12	10
Little Atlin	7	8	6	6
Little Salmon	16	16	19	19
Mayo	19	13	16	18
Michie	5	2	4	4
Quiet	14	12	11	11
Sekulmun	6	17	15	12
Snafu	3	3	3	2
Taye	1	1	1	1
Twin	8	9	8	8
Wellesley	2	6	2	3
Wolf	17	15	14	17

than any of the other lakes and Ethel Lake was a large outlier (Table 4; Fig. 6). If these two high values were removed, the correlation improved significantly (Table 4). Since Ethel Lake contains large populations of *Rhizosolenia* sp., it appears that this diatom has a low carbon content per cell, suggesting that the equation of Strathmann (1967) for diatoms is not suitable for estimating the carbon content of phytoplankton communities which are dominated by this species or other large vacuolated diatoms. The correlation between PHC and PP was also significant and informative (Table 4). The most prominent outlier was again Ethel Lake, which provides further confirmation that *Rhizosolenia* cells have a relatively low carbon content.

Chl levels under ice were higher than average summer Chl in 5 of the 10 lakes sampled, yet phytoplankton numbers and PHC were considerably lower than in summer in all except Jojo Lake. Since Jojo Lake had virtually no snow cover, we conclude that substantial production under ice was occurring there, and possibly lesser under-ice production was occurring in some of the other lakes with relatively light snow cover. Phytoplankton communities under ice and snow cover are highly shade adapted and have a high cellular Chl content. Consequently, the high Chl values recorded under ice in some lakes in this and other studies (Laperriere et al. 1975) may cause actual biomass levels to be overestimated. Direct production measurements or direct phytoplankton counts are necessary to determine if substantial production is actually occurring or if biomass is accumulating.

Trophic Status of Study Lakes

We conclude that most lakes in this study are currently oligotrophic, with some in the mesotrophic range. When the lakes were ranked using three indicators of trophic status (TP, Chl, and bacteria), Taye Lake was ranked highest by all three variables (Table 5). Taye Lake and several of the other higher ranked lakes (Snafu, Wellesley, Michie, Dezadeash) may be considered mesotrophic and the remainder as oligotrophic. The lakes lie on the northern extension of the Rocky Mountain

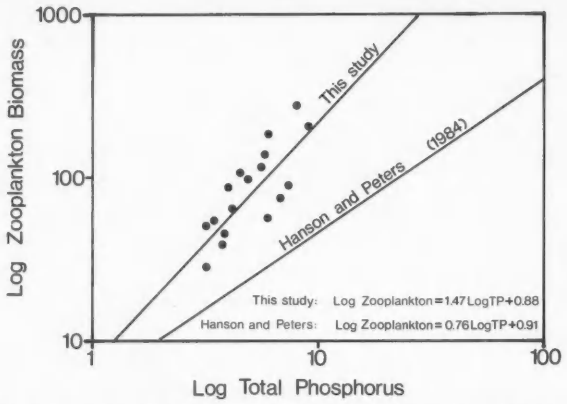

FIG. 7. Log zooplankton biomass (μg dry wt $\cdot L^{-1}$) regressed with log TP concentration ($\mu g \cdot L^{-1}$).

trench, and on the basis of average Chl levels, are more productive than subarctic lakes lying on the Canadian Shield in Labrador (Duthie and Ostrofsky 1974) but less productive than Prairie parkland lakes in northern Alberta (Prepas and Trew 1983) and temperate Shield lakes in northwestern Ontario (Schindler et al. 1978). They are also, in terms of Chl levels, less productive than lakes in northern Saskatchewan and Manitoba (Rawson 1960; Hecky and Guildford 1984).

On the basis of bacterial standing stocks, which we believe to be the best variable for estimating lake productivity, the Yukon basin lakes are more productive than large interior plateau Fraser River lakes in British Columbia (Stockner and Shortreed 1983) and far more productive than the fast-flushing British Columbia coastal monomictic lakes (Stockner and Shortreed 1985). Levels of zooplankton biomass in Yukon basin lakes are among the highest observed on the western slopes of the Rocky Mountains (Stockner and Shortreed 1983, 1985), and this we attribute to very low densities of planktivorous fish (Lindsey et al. 1981). Hanson and Peters (1984) reported a highly significant correlation ($r^2 = 0.72$, $n = 49$, $p < 0.01$) between zooplankton biomass and TP in a data set consisting of North American, European, and African lakes. In our lakes a significant correlation also existed between these variables, but the slope of the regression was substantially higher, which is further evidence that zooplankton biomass is not only high in our lakes, but is an underutilized food resource (Table 4; Fig. 7). This factor represents an important "bottleneck" to overall lake metabolism or "trophic efficiency" and may be the most important single factor constraining the growth and ultimate yield of fish populations in Yukon lakes. Not only is zooplankton biomass high, but the mean size of individuals in populations is greater than in Fraser River and coastal lakes where planktivorous fish populations are large (Stockner and Shortreed 1983), again suggesting a paucity of vertebrate and invertebrate planktivores in Yukon lakes (Brooks and Dodson 1965; Henrikson et al. 1980; Wright and Shapiro 1984). Martin (1966, 1970) has demonstrated that additions of planktivorous fish can result in increased lake trout size and growth rates. Carefully controlled introductions of planktivorous fish such as kokanee (*Oncorhynchus nerka*) would possibly vastly improve energy flow and trophic efficiency in Yukon lakes and we believe would ultimately result in increased yields of harvestable fish, notably lake trout.

Acknowledgments

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Accumulation of Cadmium by White Suckers (*Catostomus commersoni*) in Relation to Fish Growth and Lake Acidification

Leah I. Bendell-Young and Harold H. Harvey

Department of Zoology, University of Toronto, Toronto, Ont. M5S 1A1

and Jeffrey F. Young

Division of Microstructural Sciences, National Research Council of Canada, Ottawa, Ont. K1A 0R6

Bendell-Young, L. I., H. H. Harvey, and J. F. Young. 1986. Accumulation of cadmium by white suckers (*Catostomus commersoni*) in relation to fish growth and lake acidification. Can. J. Fish. Aquat. Sci. 43: 806–811.

The liver, kidney, muscle, and bone tissues of white suckers (*Catostomus commersoni*) captured from six lakes in south-central Ontario were analyzed for Cd content. The lakes ranged in pH from 4.8 to 6.4 and contained elevated Cd concentrations in the recently deposited sediments. Cd was found to be bioaccumulating in the livers of fish from both acid and circumneutral lakes, with fish from (acid) George Lake (ages 2–5) and (neutral) Red Chalk Lake (ages 7–14) containing similar concentrations. Calculated growth constants for each of the six populations revealed considerable variations in fish growth rates. A method is presented which represents the age, weight, and tissue Cd concentrations data for the six populations such that interlake comparisons of metal bioavailability can be made with the possible effects that the different fish growth rates may have on rates of metal accumulation factored out. When presented in this manner, our results imply that, on the linear portion of the growth curve, the growth rates of each population, and not effects due to lowered lake pH, can account for the concentrations of Cd in five of the six fish populations. Therefore, since tissue-metal concentrations in fish from stressed lakes will be dependent on both metal bioavailability and fish growth rates, it is essential that these be reported together.

Les tissus hépatiques, rénaux, musculaires et osseux de meuniers noirs (*Catostomus commersoni*) capturés dans six lacs du centre-sud de l'Ontario ont fait l'objet d'un dosage du cadmium. Le pH de ces lacs se situait dans la gamme de 4,8–6,4 et les sédiments récemment déposés présentaient des teneurs élevées en Cd. Il y avait bioaccumulation du Cd dans le foie des poissons des lacs acides et des lacs à pH presque neutre. Les teneurs en Cd des poissons (âge : 2–5) du lac George (acide) et de ceux (âge : 7–14) du lac Red Chalk (neutre) étaient semblables. Les constantes de croissance calculées de chacune des six populations indiquaient l'existence d'écarts considérables entre les taux de croissance. Les données relatives à l'âge, au poids et aux concentrations tissulaires de Cd des six populations sont présentées de façon à permettre la comparaison entre les lacs des valeurs de biodisponibilité du métal tout en éliminant par factorisation les effets possibles de la variabilité des taux de croissance sur les taux d'accumulation du métal. Présentés de la sorte, nos résultats indiquent, pour la partie linéaire de la courbe de croissance, que ce sont les taux de croissance de chacune des populations et non les effets de la baisse du pH des lacs qui peuvent expliquer les concentrations de Cd chez les poissons de cinq des six populations. Les concentrations du métal dans les tissus des poissons habitant les lacs en acidification étant fonction de la biodisponibilité du métal et du taux de croissance des poissons, il est donc essentiel que ces deux paramètres soient signalés conjointement.

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The increased concentrations of such metals as Mn, Al, and Cd in acid lakes owing to the leaching of metals from the watershed and the acid-induced retention of the trace metals in the water has been noted by many researchers (Dickson 1975; Henrikson and Wright 1978; Schindler et al. 1980; Wood 1980). As well, the long-range transport of heavy metals can contribute to the overall elevation of metals in lake water (Jeffries and Snyder 1981). This latter fact has been recently demonstrated by Evans et al. (1983) and Wong et al. (1984) for several acid and circumneutral lakes in south-central Ontario, with the newly deposited sediments of these lakes containing elevated Cd concentrations attributable to this origin.

Since Cd bioaccumulates in the liver and kidney of fish exposed to a point source of this metal (McFarlane and Franzin 1980; Badsha and Goldspink 1982; Ney and Van Hassel 1983), it is likely that fish from lakes in south-central Ontario exposed to anthropogenic sources of Cd also accumulate this metal in their tissues. Further, the preliminary results of K. Suns (Tri-Academy Committee on Acid Deposition 1985) implied that Cd accumulation in fish tissue was pH related. Thus, fish from acid lakes in south-central Ontario may be accumulating Cd at a faster rate than fish from circumneutral lakes. The objective of this study was to determine the role that lake pH has on the accumulation Cd in white suckers (*Catostomus commersoni*).

The rate of fish growth is known to influence the rate of

TABLE 1. Lake morphometry plus water and sediment chemistry for the six study lakes. Analyses courtesy of Ontario Ministry of the Environment except for pH and alkalinity which were measured in the field. TIP = total inflection point alkalinity; DOC = dissolved organic carbon. Cd water concentrations at present detection limits ($<0.2\ \mu g \cdot L^{-1}$) are too unreliable for interlake comparisons. Sediment Cd concentrations are means of the uppermost centimetre of sediment at three to five different sites within each lake.

Lake	Mean depth (m)	Area (ha)	pH	Alk TIP ($\mu eq \cdot L^{-1}$)	Cond. ($\mu S \cdot cm^{-1}$)	DOC ($mg \cdot L^{-1}$)	Sediment ($\mu g \cdot g^{-1} \pm$ SD)	Cd (n)
George	18.6	147.9	4.8	−3.2	31	1.5	3.5 ± 2.0	(3)
King	2.6	29.1	5.0	−3.5	26	5.6	2.1 ± 0.6	(3)
McDonald	3.0	44.0	5.2	10.9	27	6.7	2.1 ± 0.6	(3)
Crosson	8.4	56.8	5.3	0.3	27	4.0	1.6 ± 0.7	(5)
Red Chalk	14.2	56.9	6.3	64.0	28	2.8	2.5 ± 0.4	(5)
Harp	12.4	66.9	6.4	116.0	36	4.5	1.5 ± 0.8	(5)

TABLE 2. Weight, age, and the growth rate constant K for white suckers captured from the seven study lakes (N_1 = number of fish captured in the present tissue-chemistry survey; N_2 = number of fish used in determining the K value).

Lake	N_1	Weight range (g)	Age range (yr)	K	N_2
George	18	345−800	2−5	1.64	51
King	19	450−860	4−12	0.24	87
McDonald	10	83−383	2−5	0.75	20
Crosson	6	277−1220	2−6	0.31	67
Red Chalk	14	650−1650	7−14	0.48	200
Harp	18	258−940	3−8	0.52	400

accumulation and final tissue concentrations of a particular metal (Scott 1974; Norstrom et al. 1976). Fish growth rate is profoundly affected by the processess of lake acidification. For example, increased growth rates have been observed for rock bass (*Ambloplites rupestris*) (Ryan and Harvey 1977), juvenile yellow perch (*Perca flavescens*) (Ryan and Harvey 1980), Eurasian perch (*Perca fluviatilus*) (Almer et al. 1974), and brook trout (*Salvelinus fontinalis*) (Schofield 1976). Decreased rates of growth have been noted for adult yellow perch (Ryan and Harvey 1980) and for white sucker (Beamish 1974). Thus, there are sufficient variations in growth rates among acid-stressed fish that rates of metal accumulation could be significantly different due to this effect alone.

We present a method which factors out the possible contribution that the rate of fish growth may have on metal accumulation in white suckers. To do this, the two parameters, the rate of Cd accumulation and the growth rate of white suckers, were derived from age, weight, and measured Cd concentrations. The ratio of these two parameters allowed us to assess the role of lake pH on the accumulation of Cd in white suckers.

Study Area and Methods

Five study lakes in the Muskoka−Haliburton region and one from the La Cloche Mountain area of south-central Ontario were chosen, based on known water and sediment chemistry and previous knowledge of existing fish populations (Harvey and Lee 1980; Fraser and Harvey 1982; Smith 1983; Trippel 1984). Of these lakes, four were considered acid (based on the Swedish criterion that an acid lake has a pH < 5.5 (Anonymous 1979)) and two circumneutral (pH > 6.0) (Table 1).

Sediment chemistry for Red Chalk, Harp, and Crosson lakes was obtained courtesy of the Ontario Ministry of the Environment (Smith 1983). Sediments from George, McDonald, and King lakes were collected and analyzed by the methods of Smith (1983).

White suckers were collected from each of the six lakes by overnight gill netting. Eighty-five netted white suckers were sampled for weight, length, and sex. Fish age was determined by fin-ray section and scales were used to confirm the first fin-ray annulus (Table 2). Fish were placed on ice and immediately transported to the laboratory for tissue removal with glass knives and instruments.

The liver and kidney (approximately 0.25 g dry weight each), a subsection of expaxial muscle (approximately 0.3 g dry weight each), and three to five caudal vertebrae (approximately 0.1 g dry weight) immediately dorsal to the posterior of the base of the anal fin (Nos. 8−13) were removed from all fish for metal analysis. All tissues were dried to a constant weight for 36 h at 60°C. Bone samples were cleansed of all remaining muscle tissue by soaking overnight in hexane and then sonicating for 1 h, rinsing with double-distilled demineralized water (DDDW), sonicating in DDDW for 1 h, rinsing, and drying to constant weight. All samples were digested to dryness with a 4:1 HNO_3−$HClO_3$ mixture for approximately 8 h at 300°C. The digests were made up to a 10-mL volume with DDDW except the bone samples which were diluted to 20 mL with DDDW to avoid matrix problems with the higher concentrations of Ca and P that were present. Samples were analyzed for Cd by atomic emission spectrophotometry within 24 h of sample dilution using the methods of Brzezinska et al. (1984).

Accuracy and reproducibility of the tissue analysis was measured by the inclusion of a National Bureau of Standards (NBS) bovine standard whose matrix most closely resembled that of the samples. The NBS certified values for Cd were 0.44 ± 0.06 $\mu g \cdot g^{-1}$. Experimentally determined values were 0.43 ± 0.08 $\mu g \cdot g^{-1}$ ($N = 11$). The experimental limit of detection for Cd concentrations in the fish tissue was 0.6 $\mu g \cdot L^{-1}$.

Data Analysis

Values obtained from the tissue analyses were corrected for background interferences where necessary and converted to micrograms per gram dry weight of sample. Statistical analyses were carried out through SAS (Helwig and Council 1979), made available through the University of Toronto computing services. Homogeneity of group variances for the white sucker livers were verified ($P < 0.05$) through the method of Levene's test prior to an one-way analysis of variance

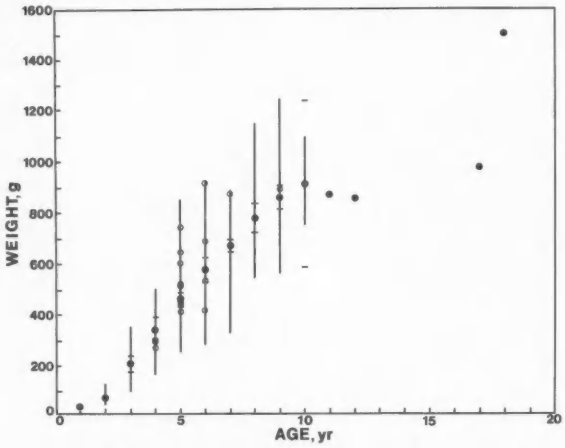

FIG. 1. Weight vs. age for Harp Lake white suckers (N = 400). Mean ± 95% C.I., plus ranges for each year are presented. Open circles represent white suckers captured in the present tissue-chemistry survey (N = 18).

(ANOVA) between elemental means. Where significant differences occurred ($P < 0.05$), Duncan's multiple comparisons were applied to indicate where they occurred ($\alpha = 0.05$). Since the fish kidney values were highly skewed, values were analyzed with nonparametric methods: a Kruskal–Wallis test was used to determine differences between fish populations ($P < 0.05$), and Scheffe's test for unequal sample sizes was used to determine where the differences occurred ($\alpha = 0.05$). To determine if Cd concentrations in the tissues were correlated significantly with fish weight ($P < 0.05$), Pearson's product correlation coefficients were calculated. Because liver Cd concentrations were correlated with fish weight in the six white sucker populations, linear regressions between liver Cd concentrations (micrograms per gram) versus fish wet weight were calculated for each of these populations.

Determination of Growth Rates

Growth rates for each white sucker population were determined through the method of Ricklefs (1967); raw weight data were replaced by conversion factors which transformed growth curves into straight lines whose slopes were measured graphically and were proportional to the overall growth rate. The equation that gave the best straight-line fit for the converted weight versus age data was used to describe the growth rates of the sucker populations. Three growth equations were tested: the logistic, the Gompertz, and the von Bertalanffy. Of these three, the logistic equation best described the growth characteristics of the fish populations and therefore was used in determining rate constants for each of the populations.

The growth rates of our sample were compared with a partial sample of the more extensive data for the same lakes presented by Harvey and Lee (1980). Because growth rates of the populations had not changed significantly (Fig. 1), all growth rates were determined from 1979–80 weight–age data.

Growth rates as defined by the logistic equation are given by

$$(1) \quad W = W_a/(1 + \exp(-K(t - t_i)))$$

where W = the weight of the fish, W_a = the asymptotic weight of the fish, K = a constant, proportional to the specific rate of growth, t = age in years, and t_i = the age required to reach half the maximum growth (i.e. half the asymptotic weight). Values of K for the individual populations are presented in Table 2.

TABLE 3. Mean Cd concentrations (± SD) and range in liver and kidney and muscle of white suckers (since kidney Cd concentrations were highly skewed, only ranges are presented). Means for a given measure for liver not followed by the same letter are significantly different ($\alpha = 0.05$, Duncan's test). Ranges for kidney values not followed by the same letter are significantly different ($\alpha = 0.05$, Scheffe's test). LoD = limit of detection.

Lake	Liver	Kidney ($\mu g \cdot g^{-1}$)	Muscle
George	3.4 ± 2.7 ab (1.5–7.0)	11.1–45.5 a	(0.1–0.7)
King	2.5 ± 1.3 bc (0.5–5.6)	7.8–17.9 b	(<LoD–0.3)
McDonald	0.4 ± 0.2 d (0.1–1.0)	0.9–6.0 c	<LoD
Crosson	2.8 ± 0.8 b (1.7–3.7)	9.1–22.0 b	(<LoD–0.8)
Red Chalk	4.7 ± 4.0 a (0.9–16)	11.0–71.0 a	<LoD
Harp	2.3 ± 1.1 bc (0.9–4.6)	5.8–31.4 b	<LoD

Results

Cd Concentrations in Sediments and Fish

Cd sediment concentrations at the surface–water interface (1 cm depth) in the six lakes ranged from 1.6 ± 0.7 to 3.5 ± 2.0 $\mu g \cdot g^{-1}$ dry mass and were not significantly different among the six lakes ($P > 0.4$) (Table 1).

Generally, Cd concentrations were greater in the kidney of the fish, with this tissue containing three times the concentrations of the metal as compared with the liver (Table 3). White suckers from (circumneutral) Red Chalk Lake and (acid) George Lake had greater liver and kidney Cd concentrations ($\alpha = 0.05$) compared with the other four lakes. Cd was found to bioaccumulate in the liver of all six fish populations (Fig. 2). Muscle Cd concentrations were at the limit of detection and were considered too unreliable to make interlake comparisons. Cd was not detected in fish vertebrae.

Growth Rates

Growth constants for the individual white sucker populations were calculated from the logistic equation (Table 2). For the six sucker populations the calculated growth constants (K) were as follows: George ⩾ McDonald > Red Chalk = Harp > Crosson > King.

Accumulation of Cd in the White Sucker in Relation to Growth and Metal Bioavailability

In this section we show quite generally how age, weight, and [Cd] data can be represented in a manner such that interpopulation comparisons of environmental factors affecting the rate of Cd accumulation can be made, independent of the population specific growth rates. The following derivation assumes that the total amount of Cd in the liver of the white sucker is

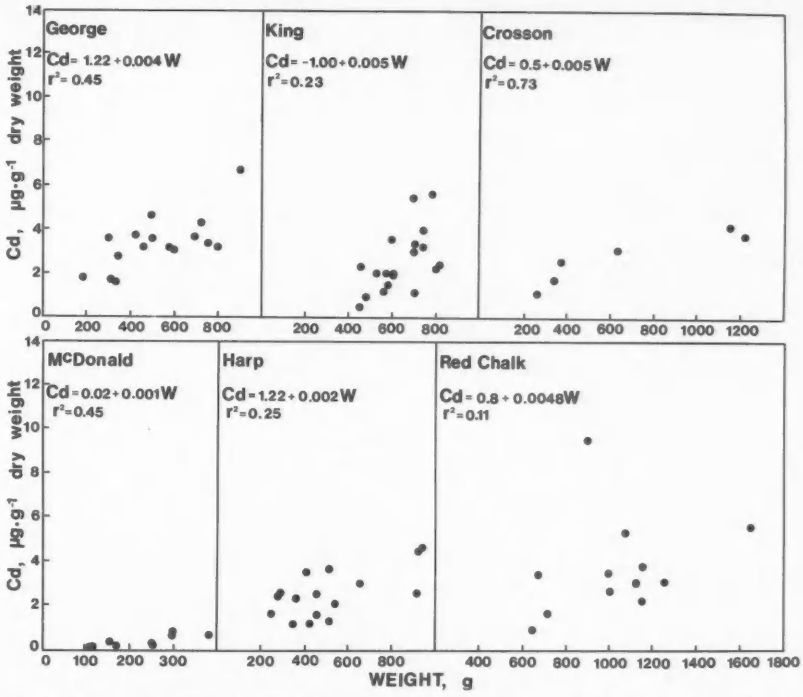

FIG. 2. Linear regressions for liver Cd concentrations vs. fish wet weight for the six white sucker populations. All regressions are significant at $P < 0.05$, with the exception of that for Red Chalk Lake fish which was not significant ($P = 0.1$).

only a function of the weight of the fish (where the type of food eaten is independent of age) and metal bioavailability in both acid and circumneutral waters. Mathematically this can be described as

$$(2) \quad \text{Cd in the liver of the fish} = f(\text{Bioavailability, Weight}) = f(B, W)$$

where the two factors, bioavailability and weight, are assumed to be independent of each other. Here, Cd is in grams and f is an unknown function of metal bioavailability and fish wet weight.

The change in Cd in the fish liver over time (grams per year) is defined as

$$(3) \quad \frac{d\text{Cd}}{dt} = \frac{\partial \text{Cd}}{\partial B}\bigg|_W \frac{dB}{dt} + \frac{\partial \text{Cd}}{\partial W}\bigg|_B \frac{dW}{dt}$$

where $\dfrac{\partial \text{Cd}}{\partial B}\bigg|_W$ = the partial change of Cd given a change in metal availability with weight held constant, $\dfrac{\partial \text{Cd}}{\partial W}\bigg|_B$ = the partial change of Cd given a change in weight where metal availability is held constant, dB/dt = the absolute rate of change of metal bioavailability, and dW/dt = the absolute rate of change of weight.

Assuming that for a given lake, the absolute metal availability does not change significantly over the life time of the fish, then for each of the fish populations taken individually, dB/dt can be set to 0. Therefore, for a given white sucker population:

$$(4) \quad \frac{d\text{Cd}}{dt} = \frac{\partial \text{Cd}}{\partial W}\bigg|_B \frac{dW}{dt}$$

or

$$(5) \quad \frac{\dfrac{d\text{Cd}}{dt}}{\dfrac{dW}{dt}} = Z\{\text{Bioavailability, } W\}.$$

Thus, if the values of $d\text{Cd}/dt$ and dW/dt are derived from experimental data and plotted versus W for various fish populations, any differences (within this model) in the resulting plots must be attributable to differences in the availability of the metal among the six lakes. It then remains to correlate the interlake similarities and differences with pH data in order to determine if lake acidity enhances metal accumulation via an increase in bioavailability. Note that at this stage, there is no restriction as to the dependence of growth rate on the age of the fish populations, other than that the growth rates must be greater than 0.

It is conceivable that the dependence of the function $Z\{B, W\}$ on weight could be quite different at different points on the logistic growth curve. Any such dependence is of interest in its own right, but for simplicity, in this analysis we restrict ourselves to consider the form of Z only throughout the linear portion of the growth curves for each population.

How is $d\text{Cd}/dt$ extracted from the measured values of W and [Cd]? Over the linear portion of the growth curve, the dependence of W on age, t, can be expressed as

$$(6) \quad W(\text{fish}) = C_1 \cdot t_i + C_2$$

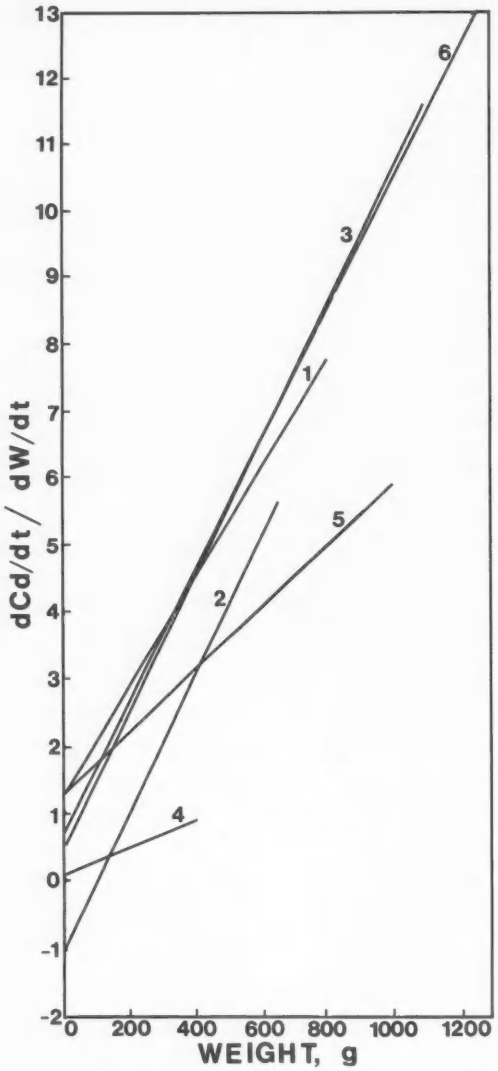

FIG. 3. Relative bioavailability factor as defined by eq. (5) for six study lakes. 1, George Lake; 2, King Lake; 3, Crosson Lake; 4, McDonald Lake; 5, Harp Lake; 6, Red Chalk Lake.

where $C_1 = W_a K/4$ and $C_2 = W_a/2 - W_a K t_i/4$ which follows from the Taylors' expansion of the denominator in eq. (1) for small values of the exponential argument. The total amount of Cd (grams) in the fish liver is given by

(7) $\quad \mathrm{Cd} = rW(\mathrm{fish}) \cdot [\mathrm{Cd}]$

where the wet weight of the liver is directly proportional to the wet weight of the fish, such that $W(\mathrm{liver}) = rW(\mathrm{fish})$. (For example, for Red Chalk Lake fish: liver weight = 0.003 (fish wet weight) − 0.141; $P < 0.005$; $R = 0.5$).

In this study the Cd concentration was experimentally determined in terms of $W(\mathrm{fish})$, i.e.

(8) $\quad [\mathrm{Cd}] = A(W(\mathrm{fish})) + B$ (from Fig. 2)

and on substitution into eq. (7) we get for Cd:

(9) $\quad \mathrm{Cd} = rW(\mathrm{fish}) \cdot (A(W(\mathrm{fish})) + B).$

Using the form of eq. (6) for the time dependence of $W(\mathrm{fish})$ in eq. (9), $d\mathrm{Cd}/dt$ can be directly obtained by differentiation, yielding

$$(10) \quad \frac{d\mathrm{Cd}}{dt} = r(2AC_1(C_1 t + C_2) + BC_1)$$

or

$$(11) \quad \frac{d\mathrm{Cd}}{dt} = r(2AC_1 W(\mathrm{fish})) + BC_1).$$

The values of C_1, A, and B extracted from the data were used in eq. (6) and (11) to obtain $d\mathrm{Cd}/dt$ (grams per year) and the growth rate, dW/dt, for the six fish populations. The ratio of $d\mathrm{Cd}/dt$ to dW/dt was then plotted for each lake (Fig. 3). Referring back to eq. (5), the form of the $(d\mathrm{Cd}/dt)/(dW/dt)$ versus W plots should provide a measure of the Cd bioavailability in a given lake. From Fig. 3 we conclude that Cd bioavailability is essentially the same for all lakes with the exception of McDonald Lake. Thus, the differences in Cd concentrations in the livers of five of the six white sucker populations can probably be attributed more to different rates of fish growth than to varying metal bioavailability, such as due to pH.

Discussion

This study has shown that (1) Cd is bioaccumulating in the livers of white suckers inhabiting lakes in south-central Ontario, (2) the accumulation of Cd by the six white sucker populations was proportional to the respective rates of fish growth, and (3) Cd bioavailability did not vary over the wide range of lake pH studied.

Comparison of the growth rates for the six white sucker populations showed that white suckers in George Lake had growth rates three times those of Red Chalk Lake. King Lake white suckers had growth rates one-half those of both Harp and Red Chalk lakes. At any given weight, the accumulation of Cd (grams per year) is also three times greater in George Lake white suckers, compared to circumneutral Red Chalk Lake suckers. In fact, at any given weight, the ratio of Cd accumulation between any of the five lakes is equal to the ratio of the respective growth rates. This, interpreted within the assumptions used to derive the mathematical expression describing the accumulation of Cd by the white suckers, as well as the similar sediment Cd concentrations between the study lakes, allows us to conclude that the bioavailability of Cd is the same among these five lakes.

The difference in the McDonald Lake data for Z suggests that Cd is less available to these fish. McDonald Lake is unique among the lakes of the set in that it is a small, shallow, highly organic acid lake, with the majority of the lake area supporting aquatic macrophytes and sphagnum moss. Ionic Cd may have been rendered biologically unavailable relative to the other five study lakes owing to the weak chelating ability of Cd^{2+} (Shephard et al. 1980). This postulate is contradicted by that of Ramamoorthy and Blunhagen (1984) who found that the presence of organic matter enhanced the uptake of Cd in fish. In their study, whole fish were analyzed for metal content; whether the ion was ingested can only be determined through tissue specific analyses. For example, McFarlane and Franzin

(1980) studied the bioaccumulation of Cd in the livers of northern pike (*Esox lucius*) and white sucker and found no relationship between the gut content of Cd and the Cd content of the target organ.

The uniformity in the bioavailability of Cd over a wide range of lake pH allowed us to conclude that rates of fish growth were an important contributor to the accumulation of metals in the white suckers from both acid and circumneutral lakes. It is likely that as there is a wide variation in growth rates among acid-stressed fish, the accumulation of metals by these fish also will be varied; specifically, the accumulation of metals by acid-stressed fish will be facilitated under conditions favouring their rapid growth. Further, faster-growing acid-stressed fish may have a greater susceptibility to the toxic effects of trace metals and show signs of metal toxicity earlier than slower-growing acid-stressed fish. Finally, since tissue-metal concentrations in fish from stressed lakes will be dependent both on metal bioavailability and fish growth rates, it is essential that these be reported simultaneously. Here-to-fore this has not been the practice.

Acknowledgments

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Predation on Larval Lake Whitefish (*Coregonus clupeaformis*) and Lake Herring (*C. artedii*) by Adult Rainbow Smelt (*Osmerus mordax*)

D. H. Loftus and P. F. Hulsman

Haliburton–Hastings Fisheries Assessment Unit, Ontario Ministry of Natural Resources, Box 500, Bancroft, Ont. K0L 1C0

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Rainbow smelt (*Osmerus mordax*) predation on larval lake whitefish (*Coregonus clupeaformis*) and lake herring (*C. artedii*) in Twelve Mile Lake, Ontario, was intense in 1984. Coregonid larvae hatched in early April as smelt spawning was ending. Predation was continuous for a 7-wk period, beginning at the onset of hatching. Numbers of coregonid larvae observed in smelt stomachs were directly proportional ($p \leq 0.005$) to their abundance in the lake. During the week when the larvae were most abundant, they occurred in 93% of the smelt stomachs containing food. The corresponding average daily consumption was 8.4 larvae per smelt. Simulation of the combined effects of smelt predation and "natural" mortality indicated that mortality of lake whitefish may be 100%. Survival of herring larvae must be greatly reduced as well. Rainbow smelt became established in Twelve Mile Lake in the 1950's; their effect on larval whitefish survival may have been aggravated by intensified dipnetting of spawning lake whitefish during the 1960's. There has been little or no recruitment of young whitefish to the population since 1975, although dipnetting for adults ceased in about 1970. Our results support the hypothesis that the primary cause of recruitment failure of this whitefish population is predation by smelt.

La prédation des larves de grand corégone (*Coregonus clupeaformis*) et de cisco (*C. artedii*) par l'éperlan (*Osmerus mordax*) dans le lac Twelve Mile (Ontario) a été intense en 1984. L'éclosion des larves de corégone s'est produite au début d'avril, au moment où la saison de frai de l'éperlan se terminait. La prédation a été continue durant une période de 7 sem, depuis le début de l'éclosion des œufs. Le nombre de larves de corégone trouvées dans les estomacs d'éperlan était directement proportionnel ($p \leq 0{,}005$) à leur abondance dans le lac. Durant la semaine où les larves ont été les plus abondantes, elles se trouvaient dans 93 % des estomacs d'éperlan contenant des aliments. La consommation journalière moyenne correspondante était de 8,4 larves par éperlan. La simulation des effets combinés de la prédation par l'éperlan et de la mortalité « naturelle » a indiqué que la mortalité du grand corégone pourrait être de 100 %. Le taux de survie des larves de hareng doit être également fortement réduit. L'éperlan s'était établi au lac Twelve Mile dans les années 50, et son incidence sur le taux de survie des larves de corégone pourrait avoir été accrue par une augmentation de la pêche au carrelet du grand corégone durant le frai dans les années 60. Il y a eu peu ou pas de recrutement de jeunes corégones depuis 1975, bien que la pêche au carrelet des adultes ait cessé vers 1970. Nos résultats viennent soutenir l'hypothèse que la principale cause de l'échec du recrutement de cette population de corégone est la prédation par l'éperlan.

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Historically, Twelve Mile Lake, Ontario, supported excellent fisheries for lake trout (*Salvelinus namaycush*) and lake whitefish (*Coregonus clupeaformis*). However, in recent years anglers seeking whitefish have experienced poor success. Estimated catch-per-unit effort (CUE) for lake whitefish has declined from 0.06–0.39 fish·angler^{-1}·h^{-1} (1961–67) to 0.004 fish·angler^{-1}·h^{-1} or less (1977–84) (Ontario Ministry of Natural Resources (OMNR), unpubl. data).

Rainbow smelt (*Osmerus mordax*) first entered Twelve Mile Lake either as an unauthorized, perhaps unwitting, direct introduction, or by immigration from upstream lakes. They were established in the lake by the late 1950's and became sufficiently abundant during the 1960's to support a spring dipnet fishery. In the 1960's there was also an intensification of the traditional fall dipnet fishery for spawning whitefish, but this fishery ended in about 1970 because of poor catches and in 1976 it was declared illegal.

Aging studies on lake whitefish collected by trapnetting and gillnetting and by creel sampling on Twelve Mile Lake indicate that recruitment failure is occurring. Only 36 specimens were observed from 1981 to the end of 1984 and their mean age, as determined from scales, was 11.2 yr. None was under 9 yr. In contrast, the ages of 19 lake whitefish taken by anglers on Twelve Mile Lake in the early 1960's ranged from 5 to 9 yr ($\bar{x}$ = 7.8 yr) (OMNR, unpubl. data).

Lake whitefish recruitment problems are not confined to Twelve Mile Lake. Population declines have also occurred in other central Ontario lakes, most notably Lake Simcoe (D. O. Evans, OMNR, unpubl. manuscr.) and Elliot Lake (D. Maraldo, OMNR, pers. comm.). A common element in the histories of all three lakes has been the inadvertent introduction and subsequent colonization of rainbow smelt in their waters just prior to or around the time that lake whitefish populations began to display signs of recruitment failure. Because smelt are known predators on a variety of fish species including

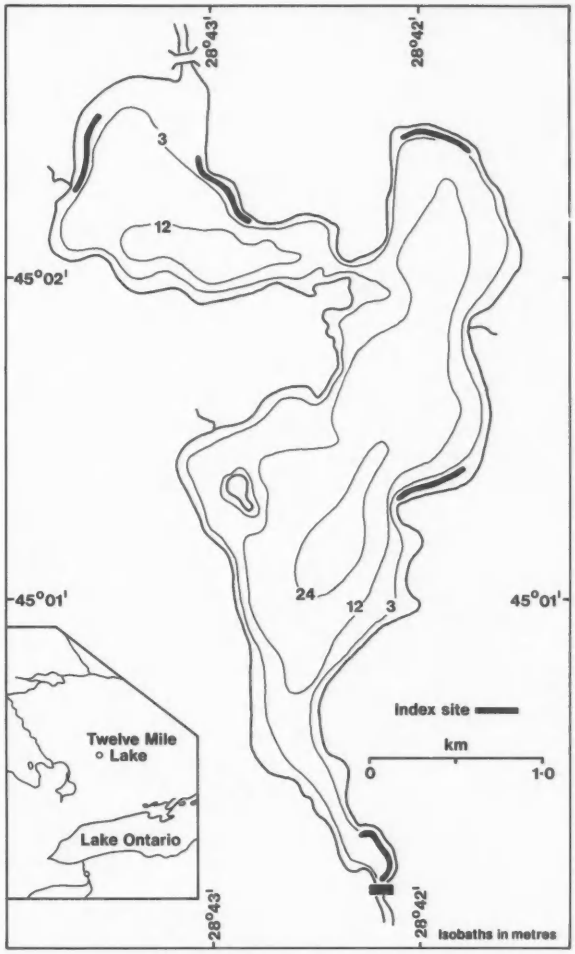

FIG. 1. Twelve Mile Lake showing index sites.

young lake herring (*Coregonus artedii*) (Selgeby et al. 1978), burbot (*Lota lota*) (Schneberger 1936; Delisle 1969), and lake trout (Hale 1959; Hassinger and Close 1984), it was considered that poor recruitment of lake whitefish in Twelve Mile Lake could have resulted from predation on the young. The major objectives of this study were to determine if smelt prey on larval coregonids in Twelve Mile Lake and, if so, whether such predation is sufficient to impair recruitment of the lake whitefish.

Materials and Methods

Study Area

Twelve Mile Lake (Fig. 1) is an oligotrophic lake located in Haliburton County, south-central Ontario (45°01′N, 78°43′W). It has a surface area of 463 ha and a maximum depth of 24 m. Its catchment is large (95 000 ha) and water replacement is correspondingly rapid (0.04 yr). Waters of the Gull and Kennesis River systems enter Twelve Mile Lake from Boshkung Lake to its north via a short channel approximatelv 50 m wide and 3 m deep. Cottage development along the shoreline is extensive.

The fish community of Twelve Mile Lake is diverse. The principal species are lake trout, lake whitefish, and smallmouth bass (*Micropterus dolomieui*). Lake herring, rainbow smelt, white sucker (*Catostomus commersoni*), yellow perch (*Perca flavescens*), pumpkinseed (*Lepomis gibbosus*), rock bass (*Ambloplites rupestris*), and brown bullhead (*Ictalurus nebulosus*) are common, but largemouth bass (*Micropterus salmoides*), brook trout (*Salvelinus fontinalis*), and burbot are rare. Other species present include slimy sculpin (*Cottus cognatus*), ninespine stickleback (*Pungitius pungitius*), trout-perch (*Percopsis omiscomaycus*), spottail shiner (*Notropis hudsonius*), common shiner (*N. cornutus*), and bluntnose minnow (*Pimephales notatus*).

Sampling Procedures

Larval fish in Twelve Mile Lake were collected using a limnetic fry sampler with an opening diameter of 80 cm and a tapered 3.0-m body constructed of 500-μm^2 polyester mesh. A 7-kg weight was used in place of a cable depressor. Tow speed was measured using a flowmeter mounted in the net opening. The sampler was deployed beside the boat by means of a tubular steel frame.

Larval fish were collected from Twelve Mile Lake from 1982 to 1984. Sampling began at ice-out each year and was continued at weekly intervals until the end of May or early June. Single samples were routinely collected at each of five index sites (Fig. 1). The net was towed at the surface for 5 min in a path parallel to shore in water about 1.5 m deep. The average tow speed was 66 ± 9 $cm \cdot s^{-1}$ (±SD). Tows were completed between 10:00 and 14:00. Samples were collected at additional sites in mid-April each year to gain an impression of the spatial distribution and abundance of larvae at that time. Between 7 March and 11 April 1984 we also collected weekly samples at the inlet to Twelve Mile Lake by lowering the net into the water from an overhead bridge and keeping it stationary in opposition to the current. The data obtained were used to determine the approximate hatching dates of lake whitefish and lake herring.

Captured fish larvae were preserved immediately in 10% formalin and later transferred to 5% formalin.

Adult smelt in Twelve Mile Lake were sampled weekly between 3 April and 13 June 1984. Monofilament nylon gillnet in 15.2-m panels with mesh sizes of 1.3, 1.9, 2.5, and 3.2 cm were fished for a single 20-h period each week. Nets were reset, if necessary, to obtain a minimum weekly sample of 20 smelt specimens.

All smelt were injected with 10% formalin upon removal from the gillnet. Fork length, weight, sex, and maturity were recorded for a random sample of 20 smelt each week. Scale samples were taken from these individuals for age determination. Stomachs of all smelt were excised and preserved in 10% formalin.

Smelt stomach contents were examined under a binocular microscope and all fish present were identified to species. Larval lake whitefish and lake herring were separated on the basis of their size and pigmentation (Hart 1930; Pritchard 1930; Faber 1970). The species composition of unidentifiable coregonid larvae was estimated using the ratio of the average numbers of larval lake whitefish and lake herring identified in stomachs collected during that week.

TABLE 1. Median weekly catches of lake whitefish and lake herring in Twelve Mile Lake, expressed as numbers per 1000 m^3.

Week	Lake whitefish			Lake herring		
	1982	1983	1984	1982	1983	1984
16–22 Apr.	—	184	75	—	149	27
23–29 Apr.	39	174	46	55	283	6
30 Apr. – 6 May	0	8	6	0	46	19
7–13 May	0	0	0	0	106	13
14–20 May	0	0	0	0	19	0
21–27 May	0	7	0	0	0	0
28 May – 3 June	0	0	0	0	0	0
4–10 June	0	—	0	0	—	6

Predation Model

The hypothesis that predation by rainbow smelt on larval lake whitefish in Twelve Mile Lake is sufficient to impair recruitment of the latter was tested by means of a simple predation simulation model. For comparison, the larval lake herring data were subjected to the same simulation. The parameters of the model were initial larval abundance, initial smelt abundance, smelt netting mortality, larval mortality due to smelt predation, and larval mortality due to causes other than smelt (i.e. "natural" mortality). Initial larval abundance was estimated by pooling catch data from 44 tows made during mid- to late April 1982–84. Larval density was estimated for each of nine sectors within the lake, and corresponding abundance values were summed to estimate lakewide abundance. Assumptions were that hatching within the lake was instantaneous and that the larvae concentrated in the top metre of water in areas where water depth was 3.0 m or less. In the absence of a direct estimate of initial smelt population size in Twelve Mile Lake, we relied on published estimates from other lakes. Smelt standing crop estimates given in Baldwin (1948), O'Connor and Power (1974), and Selgeby et al. (1978) were averaged and the resulting value (25 smelt·ha^{-1}) was halved to provide a conservative estimate of the Twelve Mile Lake adult smelt population (6000 fish). Smelt fishing mortality was calculated using weekly gillnet catch data. Daily predation by individual smelt on coregonid larvae during a given week was assumed to be equivalent to the estimated average number of larvae observed in smelt stomachs during that week. This last assumption is consistent with estimates of smelt daily rations at low temperatures used by others (Selgeby et al. 1978). Simulations were run for several different "natural" daily larval mortality rates ranging from 0.01 to 0.10.

The mechanics of the simulation are as follows. Beginning with the week of 16–22 April the number of smelt removed by gillnetting S_i during that week was subtracted from the estimate of smelt population size for the previous week S_1 to estimate the number of surviving smelt S_2. Then, for each day of the week, the number of larvae dying for reasons other than smelt predation (number of larvae surviving to the start of the present day L_i × "natural" mortality rate M_n) was subtracted from L_i. Next the number of larvae lost through smelt predation (S_2 × predation rate P) was subtracted to estimate the number of larvae surviving to the end of the present day L_{i+1}. Thus

$$L_{i+1} = L_i - L_i \cdot M_n - S_2 \cdot P.$$

Appropriate estimates of the daily smelt predation rates were applied as the simulation progressed through each of the 5 wk. Several scenarios were simulated by varying the initial population sizes of adult smelt and larval lake whitefish or lake herring, and the natural mortality rate.

Results

Spring break-up on Twelve Mile Lake took place on 28 April 1982 and between 17 and 19 April in 1983 and 1984.

Median weekly catches of larval lake whitefish and lake herring at indexing sites were usually highest just after break-up (Table 1). Larvae of both species were generally most abundant in the northeastern and northwestern extremities of the lake. Tows made during April in the southern half of the lake and at offshore sites in the northern half yielded poor or null catches.

Catches of both species declined at index sites after the first week of open water although there appeared to be smaller peaks in larval lake herring abundance following the first (Table 1). Lake whitefish catches were usually poor and sporadic by the first week of May, resulting in null median weekly CUE values. Lake whitefish larvae were not captured after 12 May 1982, 24 May 1983, or 16 May 1984. Catches of lake herring larvae continued a week or two longer, but then also declined to zero.

Application of the Wilcoxon matched-pairs signed-ranks test (Siegel 1956) indicated that the catches of lake whitefish and lake herring differed significantly ($n = 28, z = 3.21, p \leq 0.05$) only in 1983 when the latter were more abundant.

Based on the combined tow data for the years 1982–84 the initial abundance of coregonid larvae in Twelve Mile Lake was estimated at 135 000 lake whitefish and 325 000 lake herring. The upper 95% confidence limits for these estimates were 400 000 and 860 000, respectively. In consideration of the imprecision of the calculated estimates and of the need for conservatism in the simulation, we arbitrarily used 400 000 lake whitefish and 600 000 lake herring as our "best" estimates of initial larvae abundance.

Four hundred and ninety-four smelt were collected in gillnets in Twelve Mile Lake in 1984. Scale ages of 226 individuals ranged from 1 to 4 yr but the majority (88%) were 2 yr. Fish in this sample ranged in size from 8.5 to 21.5 cm. They had a mean fork length of 14.4 cm and a mean weight of 19.3 g. In 1984, smelt spawned between 10 April, when 95% of the individuals examined were ripe, and 18 April, when 95% were spent (Table 2). Less than 41% of the smelt captured on 10 April or earlier were feeding, but by 25 April all stomachs contained food (Table 2). The increase in feeding activity coincided with the increase in the proportion of spent individuals in the sample.

The food types most frequently observed in smelt stomachs were larval coregonids, zooplankton (especially copepods), and dipteran pupae (Table 2). Amphipods, *Mysis relicta*, Chironomidae and Chaoboridae larvae, Ephemeroptera nymphs, and yearling smelt usually occurred less frequently but generally contributed to the smelt diet on at least half of the sampling dates (Table 2). Other items observed infrequently and occurring in stomachs on only a few occasions were horsehair worms (Gordiidae), water mites (Acari), crayfish (Decapoda), Ceratopogonidae larvae, Coleoptera, stonefly nymphs (Plecoptera), caddisfly nymphs (Tricoptera), smelt eggs, yellow perch larvae, and ninespine stickleback.

On 3 April 1984, copepods and cladocerans were present in 92% of the smelt stomachs with food. One smelt also con-

TABLE 2. Relative frequency-of-occurrence (%) of major food item types in smelt stomachs containing food during spring 1984 in Twelve Mile Lake. Reproductive condition (percent spent) is shown.

	April				30 Apr. – 6 May	May			28 May – 4 June	June	
	2–8	9–15	16–22	23–29		7–13	14–20	21–27		5–11	12–18
No. of smelt examined	141	39	37	47	24	84	22	25	39	20	16
% spent	0	5	95	96	100	100	100	—	—	—	—
% with food	37	41	78	100	100	69	64	72	72	70	88
Zooplankton	92	63	7	4		29	28	33	39	71	79
Amphipoda				4	4	2		6		7	
Mysis relicta		25	3	11	8	5		6	7	21	7
Insects	10	13	14	94	92	78	64	78	71	64	86
Chaoboridae larvae									4	29	71
Chironomidae larvae	4	6	7	2	4	2				14	14
Dipteran pupae		6	3	89	92	46	29	61	71	14	29
Ephemeroptera nymph			7	2	4	3	35	11		7	7
Smelt yearlings				6	8	7	7	11	4		
Coregonid larvae	2	13	93	38	25	19	7				
Whitefish		6	41	6	8	4					
Herring		6	28	4	13	2					

TABLE 3. Estimates of daily consumption of larval lake whitefish and lake herring by rainbow smelt in Twelve Mile Lake, 9 April – 27 May 1984.

	April			30 Apr. – 6 May	May		
	9–15	16–22	23–29		7–13	14–20	21–27
No. of smelt examined	39	37	47	24	84	22	25
Total no. of coregonid larvae	4	244	37	78	16	2	0
No. of whitefish identified	2	113	18	2	2	0	0
Estimated total no. of whitefish	3	173	30	3	11	1	0
Estimated no. of whitefish per stomach	0.08	4.68	0.64	0.14	0.13	0.04	0.00
No. of herring identified	1	43	4	43	1	0	0
Estimated total no. of herring	1	66	7	75	5	1	0
Estimated no. of herring per stomach	0.03	1.84	0.15	3.13	0.04	0.04	0.00

tained larval coregonid remains. The frequency-of-occurrence of coregonid larvae in stomachs increased to 13% on 10 April and to 93% on 18 April (Table 2). Altogether, 244 larvae were counted in stomachs of smelt collected on 18 April, an average of 8.4 larvae per stomach (containing food). In contrast, zooplankton had become a relatively unimportant part of the diet by 18 April. The occurrence of coregonid larvae declined to 38% on 25 April, while that of dipteran pupae increased dramatically to 89%. The relative contribution of larval coregonids to the smelt diet continued to decline with occurrence dropping to 25% on 2 May, 19% on 9 May, and 7% on 17 May. None were observed in smelt stomachs after that date. Throughout early May and again in late May and early June, dipteran pupae were the prey most widely utilized by smelt. Zooplankton, especially copepods and Chaoboridae larvae, were the main food types in mid-June (Table 2).

Of the 381 coregonid larvae counted in smelt stomachs, 137 (36%) were identified as lake whitefish and 92 (24%) as lake herring (Table 3). In many instances larvae were too thoroughly digested to be counted, but their remains were recognizable as small white fragments of tissue. Larval whitefish outnumbered lake herring in smelt stomachs and in larval tows between 10 and 25 April (Table 3). The predominance of lake herring in stomachs on 2 May was consistent with trawl catches on that date as well. Data presented in Table 3 on estimated numbers of whitefish or herring per smelt stomach were used in the simulation model to approximate daily predation rates.

Strong correlations existed between weekly larval lake whitefish index CUE values and the mean number of lake whitefish larvae per stomach ($r = 0.88$, $n = 5$, $p \leq 0.025$) and between larval lake herring index CUE values and frequencies-of-occurrence of lake herring larvae in smelt stomachs ($r = 0.91$, $n = 5$, $p \leq 0.025$). Of greater significance ($r = 0.99$, $n = 5$, $p \leq 0.005$) was the relation between combined index CUE values and frequencies-of-occurrence of all coregonid larvae in smelt stomachs. There was no apparent relation between the incidence of larvae in stomachs and smelt size.

The results of the predation simulation exercise indicated that, with an initial smelt population of 6000 fish and daily "natural" mortality rate of 5% among larvae, the initial abundance of both lake whitefish and lake herring would have to be greater than those estimated if some larvae were to survive (Fig. 2). The effects that errors in our estimation of initial smelt abundance, initial larval abundance, and larval "natural" mortality rates would have on the results are illustrated in Fig. 2.

Discussion

The present data on smelt feeding clearly demonstrate that predation by adult rainbow smelt on larval lake whitefish and lake herring can be intense. In Twelve Mile Lake, peak

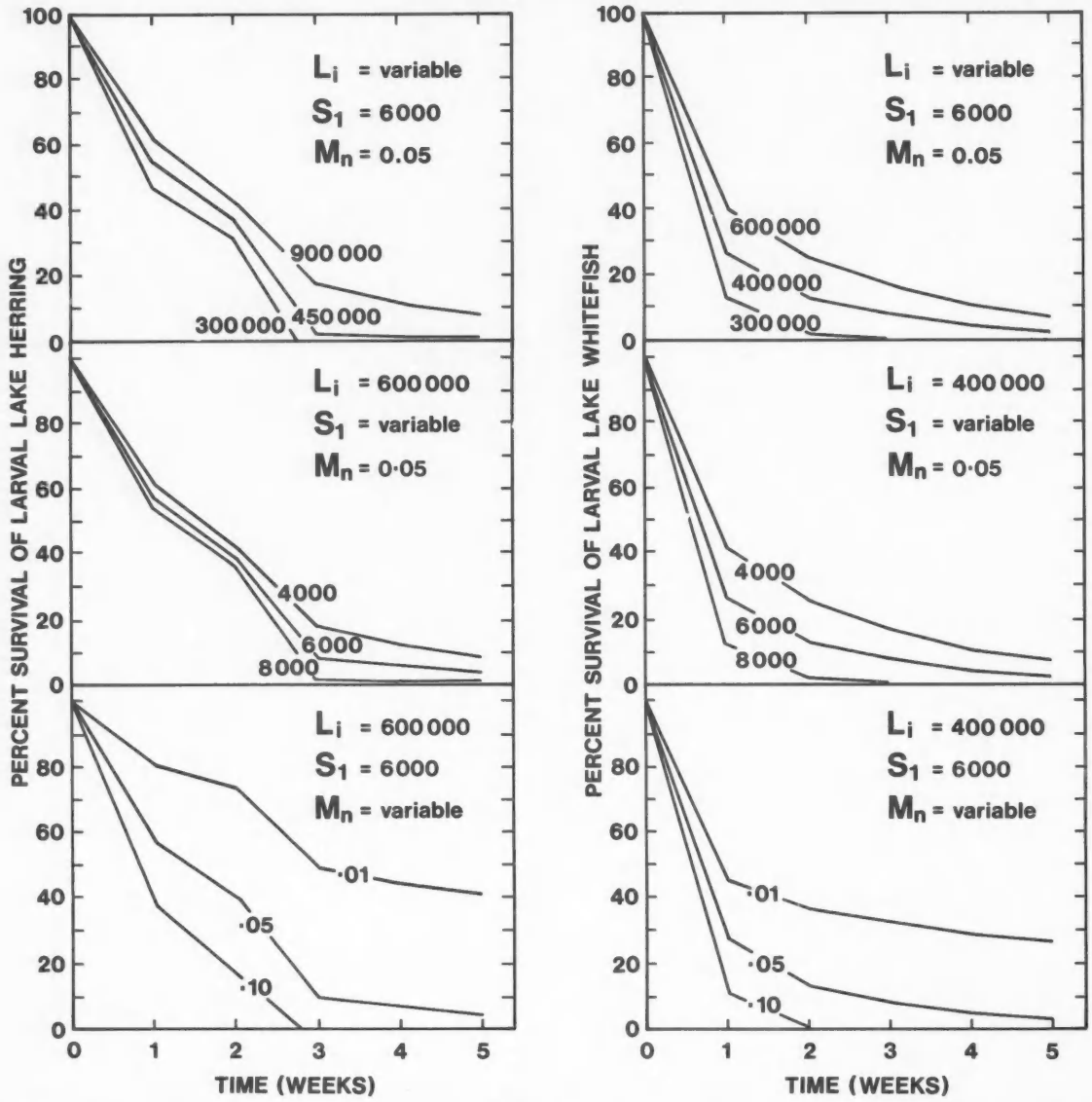

FIG. 2. Percent survival of larval lake herring and lake whitefish using different estimates of initial larval population size L_i, initial smelt abundance S_1, and natural daily larval mortality rate M_n. Daily predation rates used are provided in Table 3.

hatching activity of lake whitefish and lake herring coincided with peak smelt spawning activity. Our observations and the results of MacCrimmon and Pugsley (1979) indicate that smelt feeding activity intensifies after spawning. Newly hatched coregonid larvae are prime targets for predation at this time. Selgeby et al. (1978) examined the feeding habits of smelt following the spring hatch of lake herring in Black Bay, Lake Superior, and found that adult smelt (≥100 mm) had consumed on average 35.8 lake herring larvae.

To our knowledge, the present study is the first recorded case of smelt preying on larval lake whitefish. It is not surprising that this was observed first in a small lake, nor that predation was intense. In Twelve Mile Lake there is essentially no segregation between the coregonid larvae and adult smelt in early spring, and refugia for the larvae are lacking. In lakes like Twelve Mile Lake, coregonid larvae are probably quite attractive to the smelt because of their availability and their large size (~8.0 mg) relative to that of alternate prey. Predation may be less intense in larger lakes, such as the Laurentian Great Lakes, where the distribution of larvae in nearshore areas probably affords them some level of protection. It seems likely, however, that smelt feed opportunistically on lake whitefish larvae in large lakes just as they do in small ones such as Twelve Mile. This conclusion is supported by the results of Selgeby et al. (1978) who reported that when dense populations of smelt and herring larvae were in close contact the smelt ate herring larvae, but when densities were lower and contact less direct, no herring larvae were found in smelt stomachs. Failure of

previous studies (e.g. MacCrimmon and Puglsey 1979) to detect smelt predation on lake whitefish in large lakes may be related to sampling procedures.

The results of the simulation of smelt predation on larval lake whitefish and lake herring in Twelve Mile Lake provide strong evidence to implicate smelt as an important factor in the recruitment failure of the whitefish population. They are also consistent with events that occurred in Maine's Fish River Lakes as reported by Warner and Fenderson (1963). All eight of the Fish River Lakes once supported good lake whitefish populations, but whitefish now exist only as residual populations in the seven lakes stocked with smelt during the 1890's. Although the role it has played remains unclear, the smelt has also been regarded with strong suspicion by Great Lakes fisheries investigators, especially with respect to fluctuations in coregonid stocks (Christie 1974; Crowder 1980). In contrast, Selgeby et al. (1978) concluded that predation by smelt on herring larvae was not a major factor controlling or supressing herring stocks in the two regions they studied in western Lake Superior. Similarly, Stedman and Argyle (1985) reported that predation by rainbow smelt has apparently not had a negative effect on bloater (*Coregonus hoyi*) abundance in Lake Michigan in the recent past. They cautioned, however, that if smelt abundance were to increase, then predation by smelt could become a significant factor in the survival of juvenile bloaters.

The vulnerability of the Twelve Mile Lake whitefish population to predation by smelt may have been increased due to heavy exploitation of the stock during the 1960's. Winter angling for whitefish was popular during that period, and daily creels of 20 fish per angler were common. Also, spawning whitefish were exploited by a fall dipnet fishery. The decreased catches that brought an end to the dipnet fishery on Twelve Mile Lake in 1976 were a clear indication that the spawning stock had been greatly reduced. Subsequently, the numbers of eggs and larvae produced may have been insufficient to withstand the added stress of smelt predation.

Degradation of water quality has been cited as a factor affecting lake whitefish populations. D. O. Evans (unpubl. manuscr.) presented evidence implicating hypolimnial dissolved oxygen depletion as the cause of the recent recruitment failure of Lake Simcoe lake whitefish. In Twelve Mile Lake, however, oxygen depletion is less severe, and Lasenby (1975) suggested that it is a natural occurrence in this lake rather than a recent response to increased nutrient loading. Concentrations of total phosphorus ($0.005\ mg \cdot L^{-1}$) and total nitrogen ($0.366\ mg \cdot L^{-1}$) indicate that the degree of nutrient enrichment of Twelve Mile Lake water has been slight. Success at capturing moderate numbers of lake whitefish larvae confirms that whitefish spawning occurs successfully and that conditions are suitable for egg incubation. The availability of suitable food items and acceptable limnological conditions is further affirmed by the fact that there is some survival among lake herring larvae which have food and habitat requirements similar to those of larval lake whitefish (Hart 1930; Pritchard 1930).

We acknowledge that our predation model is a simplification of events in Twelve Mile Lake and that the results of the simulations are subject to the high degree of uncertainty associated with the parameter estimates (Fig. 2). Recognizing the imprecision of the estimates, we tried to use realistic but conservative values. For example, the use of unadjusted stomach contents data from smelt taken in overnight gillnet sets probably underestimates food consumption, even in cold water (F. P. Binkowski, Centre for Great Lakes Studies, University of Wisconsin, pers. comm.; Crowder 1980). Also, we used the upper 95% confidence limit of the stratified mean larval whitefish catch, rather than the mean itself, to estimate initial population size (400 000 fish). Use of these values in simulations gave results consistent with present conditions in the lake. This supports the view that smelt predation has a significant impact on the survival of lake whitefish and lake herring larvae in Twelve Mile Lake, and that it may have resulted in the complete elimination of the 1984 year class of lake whitefish. The model may, however, underestimate larval herring survival because it takes no account of larvae hatched and recruited to the population after April.

Continued monitoring of the Twelve Mile Lake fish community will reveal how successfully lake whitefish and lake herring populations sustain the damage smelt inflict upon recruitment. There is little doubt that smelt cause similar damage in other lakes, particularly in smaller ones where virtually all coregonid larvae are accessible to smelt and therefore vulnerable to predation. As the range of smelt in the Great Lakes region continues to expand, the cumulative damage to lake whitefish and lake herring resources may be considerable.

Acknowledgements

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Intervention Analysis of Power Plant Impact on Fish Populations[1]

Charles P. Madenjian,[2] David J. Jude, and Frank J. Tesar

Great Lakes Research Division, University of Michigan, Ann Arbor, MI 48109, USA

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Alewife (*Alosa pseudoharengus*) and yellow perch (*Perca flavescens*) abundances, estimated from monthly gillnet and trawl catches at two transects, were monitored before (1973–74) and during (1975–82) operation of the D. C. Cook Nuclear Power Plant, southeastern Lake Michigan. Intervention analysis, a technique which accounts for autocorrelated observations, and analysis of variance (ANOVA) were applied to the monitoring data to assess any plant impact beginning in 1975. Both analyses disclosed no significant power plant impacts except for gillnetted yellow perch adults. The ANOVA indicated a significant decrease in abundance at the plant-discharge transect relative to the reference transect as plant operation began, which established a plant effect; intervention analysis showed no change. When April and May catches (months of low abundance) were deleted, this plant effect was insignificant. Monte Carlo simulation showed that as the first-order autoregressive coefficient increased positively, type I error of the ANOVA *F*-test increased. However, ANOVA was more powerful than intervention analysis when a first-order autoregressive component was included. Impact assessment based only on ANOVA can result in detection of impact when actually there was no effect (type I error) when observations are serially correlated (lack independence).

L'abondance du gaspareau (*Alosa pseudoharengus*) et de la perchaude (*Perca flavescens*), évaluée à partir des prises mensuelles au filet maillant et au chalut dans deux transects, a été contrôlée avant (1973–74) et pendant (1975–82) l'exploitation de la centrale nucléaire D. C. Cook, au sud-est du lac Michigan. Les données de contrôle ont été traitées par l'analyse d'intervention, une technique basée sur des observations autocorrélées, et l'analyse de variance, depuis 1975, afin d'évaluer tout effet éventuel de la centrale. Les deux méthodes d'analyse n'ont révélé aucun effet significatif de la centrale, sauf pour les perchaudes adultes prises au filet maillant. L'analyse de variance a indiqué une baisse significative de l'abondance au transect d'évacuation de la centrale par rapport au transect témoin au début de l'exploitation de la centrale, ce qui a démontré l'effet de celle-ci sur l'environnement, alors que l'analyse d'intervention n'a révélé aucun changement. En supprimant les prises d'avril et de mai (mois de faible abondance), cet effet de centrale n'était pas significatif. La simulation de Monte Carlo a démontré que l'augmentation positive du coefficient auto-régressif de premier degré était liée à une augmentation de l'erreur de type 1 du test *F* de l'analyse de variance. Cependant, l'analyse de variance se révélait plus puissante que l'analyse d'intervention lorsque l'on tenait compte d'un facteur autorégressif de permier degré. L'évaluation des effets basée uniquement sur l'analyse de variance peut entraîner la détermination d'effets, alors qu'il n'y a en réalité aucun effet (erreur de type 1) lorsque les observations sont corrélées en série (absence d'indépendance).

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Operation of a power plant requires large quantities of cooling water with potentially adverse effects on fish populations living in the cooling water source. Withdrawal of cooling water reduces fish numbers either through impingement of adult and juvenile fish or entrainment of fish larvae and eggs. Discharge of the heated water may alter thermal regimes in the plant vicinity, and use of biocides (such as chlorine) to control biofouling may have toxic effects on fish. If these potential sources of mortality are substantial, then impact of a power plant on fish populations may be measured by monitoring fish abundance in the water body. Numerous authors (Murarka et al. 1976; Thomas and Eberhardt 1976; McKenzie et al. 1977; Thomas 1977; Skalski and McKenzie 1982) recommended a monitoring design that includes sampling at two transects: one transect close to the water intake and discharge of the plant and a reference transect, assumed to be outside the influence of plant operation. Furthermore, both transects are to be sampled regularly before (preoperational period) and during plant operation. Observations from the plant-discharge transect should be paired with observations from the reference transect, so that proportional abundance of organisms at reference and plant-discharge stations can be analyzed (Skalski and McKenzie 1982). Hence, impact can be interpreted as a statistically significant change in the proportional abundance of organisms at reference and plant-discharge stations between preoperational and operational periods.

Gore et al. (1976), McCaughran (1977), and Skalski and McKenzie (1982) recommended analysis of variance (ANOVA) for the detection of impact. Thomas (1977) discussed the limitations of ANOVA in determining change in fish abundance due to plant operation; he pointed out that the assumption of independence among observations may be violated. Furthermore, he argued that the lack of independence among observations was not overcome by analyzing the ratio of fish abundance of the two transects. Murarka et al. (1976) suggested the time series approach, namely intervention

[1] Great Lakes Research Division Contribution No. 436.

[2] Present address: Department of Zoology, University of Hawaii, Honolulu, HI 96822, USA.

analysis, as an alternative to ANOVA. However, their application of intervention analysis was limited to a preliminary examination of the phytoplankton abundance series for the Zion Plant, Lake Michigan. Millard et al. (1985) examined the same phytoplankton data and also studied, via Monte Carlo simulations, the effects of spatial and temporal correlation on the ANOVA model used to assess impact of the plant. They concluded that spatial or temporal correlation would inflate the size of the type I error; that is, the ANOVA procedure would be more likely to detect a change in the abundance proportion, when no change had actually taken place, as the degree of correlation increased. Green (1979) and Rago et al. (1983) suggested use of Monte Carlo simulation to evaluate statistical models for impact assessment.

The aims of our study were to (1) apply intervention analysis and ANOVA to the 10-yr fish abundance series for the D. C. Cook Nuclear Power Plant, southeast Lake Michigan, (2) compare results from the two analyses, and (3) study type I and type II error rates for both analyses via Monte Carlo simulation. Finally, recommendations on the use of these two statistical techniques for fisheries impact assessment will be made.

Sampling Methods

Trawling and gillnetting were performed both day and night from April to October during 1973–82. Plant operation began in 1975, so 2 yr of preoperational and 8 yr of operational data were available. Two stations at 6 and 9 m were sampled at a plant transect and two stations at corresponding depths were sampled at a reference transect approximately 7.3 km south of the plant.

Duplicate 10-min bottom tows were taken at each station using a semi-balloon 4.9-m trawl of 1.9-cm bar mesh. Tows were performed at an average speed of 5 km/h; the trawl was towed parallel to shore with one replicate taken from south to north and the other from north to south (Jude et al. 1979). Multifilament nylon experimental gill nets 160 × 1.8 m, each consisting of 12 mesh sizes from 1.3 to 10.2-cm bar mesh, were set for approximately 12 h. All gillnet catches were adjusted for a 12-h set (Jude et al. 1979).

Intervention Analysis

Serial correlation can be described as lack of independence among observations; that is, one observation is dependent on a set of previous observations. The Box and Jenkins (1976) approach to time series analysis represents a collection of several statistical techniques used to describe a wide variety of serial correlations. The autoregressive integrated moving-average (ARIMA) model is the general model assembled by Box and Jenkins. To identify an ARIMA model appropriate for a particular time series of data, several methods are available, including autocorrelation and partial autocorrelation functions, model overfitting, and residual analysis (Nelson 1973; Box and Jenkins 1976).

A common type of serial correlation for fisheries data is described by an autoregressive process of order 1 (an AR(1) process). The AR(1) process behaves such that an observation at one point in time is dependent or correlated with an observation made during the previous time period:

$$(1) \quad Z_t = \mu + \phi_1(Z_{t-1} - \mu) + a_t$$

where Z_t = value of series at time t, μ = mean of the time series, ϕ_1 = autoregressive coefficient of order 1, and a_t = residual at time t.

The ARIMA model is frequently used to model seasonal time series (Pierce 1980). Consider a series of fisheries catch data composed of monthly observations (12 observations per year) and several years in length. We may expect the series to exhibit periodic behavior with a period of 12 mo. A moving-average term of order 12 may be appropriate to model such a series (Box and Jenkins 1976); this moving-average term is the difference between the actual and predicted values of the series at a time lag of 12. Furthermore, differencing the original series by degree 12 usually results in a stationary series. This seasonal differencing is accomplished by creating a new series in which each observation is equal to an observation in the original series minus the observation in the original series 12 mo earlier (beginning with the 13th observation of the original series). In equation 2, Z_t represents the original series and W_t is the differenced series. (A stationary series is a series in equilibrium about a true mean. Stationarity is an assumption to modeling any series with autoregressive or moving-average components.) Tentatively, we have the following model for seasonality:

$$(2) \quad W_t = \theta_{12}a_{t-12} + a_t$$

where $W_t = Z_t - Z_{t-12}$, Z_t = observation of time series at time t, θ_{12} = moving-average coefficient of order 12, and a_t = residual at time t.

The intervention analysis model (Box and Tiao 1975) includes a Box–Jenkins model and an intervention imposed on the series. In our application, the intervention would be plant operation, which began in 1975. The model component which determines the response of the series to the intervention is known as the transfer function (Box and Jenkins 1976). We might envision several responses of fish abundance to plant operation. For example, if the thermal discharge physically attracted or repelled fish, then we may expect a step increase or decrease, respectively, in which ω represents the step increment in the series (Fig. 1). Suppose that plant operation affected carrying capacity of the population in the immediate plant vicinity. The response of the fish population to a change in carrying capacity may follow the S-shaped logistic curve. This curve can be approximated by a step, ramp, or first-order response (Fig. 1), depending on response speed. Guppy (*Poecilia reticulata*) populations subjected to changes in harvest rates appeared to decline or increase linearly in some cases (data from Silliman and Gutsell 1958). In other cases, the first-order response appeared to fit the data well. Entrainment and impingement could result in increased mortality and may cause a noticeable decrease in population size, similar to the response of the guppy population to increased harvest rate. In the ramp response, ω represents the slope of the line. In the first-order response, $\omega/(1 - \delta)$ equals the change in the mean abundance level, where ω is the initial increase or decrease in the series following the intervention and δ represents the rate of decay of the initial change. Responses may be delayed (Murarka et al. 1976); so besides modeling immediate responses to plant operation, we visually inspected the series for delayed response and fitted an intervention model accordingly (using one of the three transfer function models presented). Since most alewife (*Alosa pseudoharengus*) and yellow perch (*Perca flavescens*) in the plant vicinity do not mature until their third year (Jude et al. 1979), a delay in the abundance response of 2–3 yr is plausible.

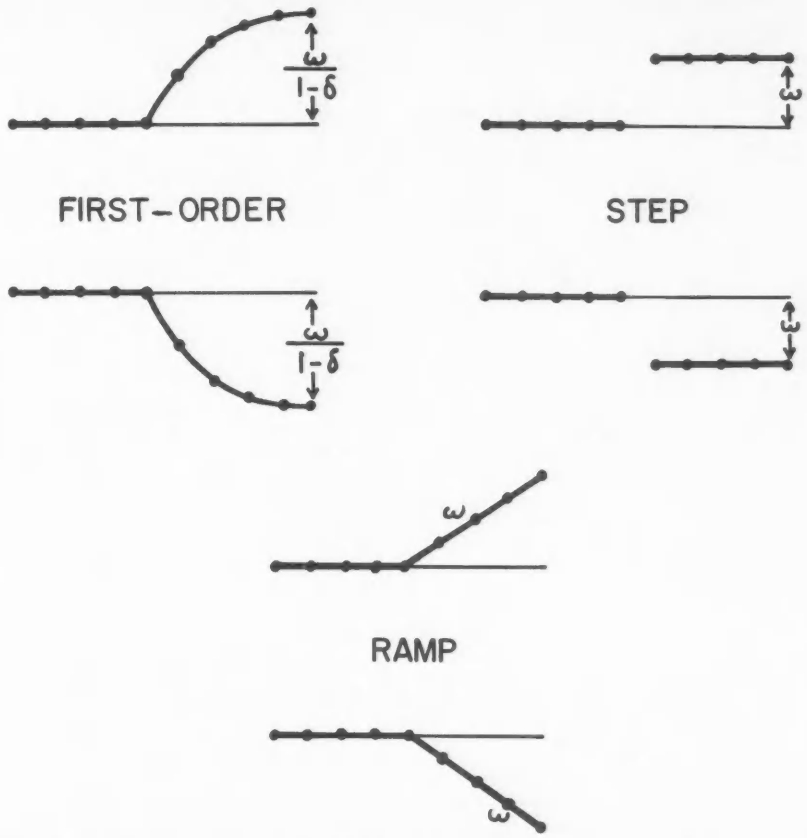

FIG. 1. Illustrations of the three types of responses considered in the intervention analysis of the fish monitoring field data for the D. C. Cook Plant, southeastern Lake Michigan (modified from Box and Tiao 1975).

Combining the transfer function with a "general" Box–Jenkins model (general for our purposes), we have

$$(3)\quad W_t = \phi_1 W_{t-1} + \theta_m a_{t-m} + F(\omega, X_t, t) + a_t$$

where W_t = value of stationary series at time t (the series may be undifferenced (if differencing was not required for stationarity) or may be differenced (differenced by degree m)), m = number of months in sampling year, ϕ_1 = autoregressive coefficient of order 1, θ_m = moving-average coefficient of order m, $F(\omega, X_t, t)$ = transfer function, ω = vector of transfer function parameters, X_t = vector of exogenous variables, and a_t = residual at time t. For a step response, $F(\omega, X_t, t) = \omega x_t$, ω is the step increment, and

$$x_t = \begin{cases} 0, \text{ for all } t \text{ before plant operation} \\ 1, \text{ for all } t \text{ during plant operation.} \end{cases}$$

Statistical Methods

Intervention Analysis and ANOVA of Monitoring Data

For both trawl and gillnet data, a time series was formed for each transect by pooling all catches for each month of monitoring effort. Series for alewife and yellow perch were formed. Due to missing observations, gillnet series included data for April through September. Trawl series included data for April through October. Months in which no sampling was performed were not considered in the analyses. If we denote total catch (number of fish) at the Cook Plant transect (plant-discharge transect) as CP and catch at the reference transect as RT, then a log difference series, $\ln(CP + 1) - \ln(RT + 1)$, was formed, where ln denotes the natural logarithmic function. Examination of the raw data indicated that seasonal fluctuation was not constant for all sampling years; rather, the seasonal fluctuation was high when average catch for the year was high and low when catch for the year was low. The seasonal effect thus appeared to be multiplicative. Consequently, the ln transformation was employed.

Intervention analysis was applied to the log difference series (also referred to herein as ratio series). In addition to the abundance series in which all age groups of fish were pooled, series were generated for young-of-the-year (YOY), yearlings, and adults (≥age 2). Age groups were determined by length–frequency analysis (Jude et al. 1979). Yearling and YOY series for gillnet abundances were not analyzed because catches were too low and infrequent. The same months were used in the age-group pooled and the age-group separated series, except for YOY. Since YOY were chiefly caught during late summer through fall, only observations from August to October were included in the YOY series.

Intervention analysis was performed on all ratio (log difference) series. Step, ramp, and first-order responses were tested. An intervention was considered statistically significant if each of the transfer function parameters was significant at $\alpha = 0.05$. For example, a ramp response was significant if the slope of the response, ω, was significantly different from zero. We assumed that distribution functions for transfer function parameters were approximated by a t-distribution (Box and Tiao 1975).

ANOVA was also applied to the ratio series and results were compared with those for the step response of intervention analysis. The ANOVA model used was comparable with the step intervention model:

$$(4) \quad Y_{ijk} = \mu + \alpha_i + \beta_j + e_{ijk}$$

where Y_{ijk} = observation for month i, plant status j, and replicate k, μ = grand mean, α_i = month effect ($i = 1, \ldots, m$), β_j = plant status effect ($j = 1, 2$ (1 = preoperational, 2 = operational)), and e_{ijk} = residual for replicate k of i, j treatment.

No interaction term was included so that the intervention model and ANOVA were directly comparable. Additionally, a two-sample t-test (for equal variances) was performed on each ratio series to compare the preoperational mean with the operational mean of the series.

Trend Analysis

Trend analysis was performed on the log-transformed series for the plant-discharge transect (the ln (CP+1) series) and for the reference transect (the ln (RT+1) series). Analysis of trends in the abundance series for both transects offers some confirmation of the ratio series results. For example, if both transect series showed similar trends, then no significant interventions would be expected in the ratio series. Furthermore, if abundances at both transects showed similar trends, trends which have occurred throughout Lake Michigan (Wells 1977; Wells and Hatch 1984), then results of the time series applications would be corroborated. The model used for trend analysis was identical to that for intervention analysis except a trend was imposed at the first observation of the series (usually April 1973) instead of an intervention imposed at the start of plant operation in 1975. The trend analysis model for the ramp response was

$$(5) \quad W_t = \phi_1 W_{t-1} + \theta_m a_{t-m} + \omega x_t + a_t$$

where W_t = value of stationary series at time t, ϕ_1 = autoregressive coefficient of order 1, θ_m = moving-average coefficient of order m, a_t = residual at time t, ω = slope of ramp (change in value of series per year), $x_t = t/m$ (time, in years, from start of series), and m = number of months in sampling year. Two trends were modeled for each plant-discharge and reference series: ramp and first-order. As in the intervention analysis case, a trend was considered significant if each of the transfer function parameters was significant (at $\alpha = 0.05$).

Monte Carlo Simulation

Monte Carlo simulations were conducted to compare the magnitudes of the type I error and type II error for both intervention analysis and ANOVA. Type I error size for a statistical test is the probability of rejecting the null hypothesis, given that it is true; size of the type II error is the probability of accepting the null hypothesis, given the null hypothesis is false. A series requiring differencing was generated with the following form:

$$(6) \quad W_t = \phi_1 W_{t-1} + 0.85 a_{t-m} + a_t$$

where $W_t = Z_t - Z_{t-m}$, Z_t = value of series (before differencing) at time t, ϕ_1 = first-order autoregressive coefficient, m = number of months in sampling year, and a_t = residual at time t.

All abundance series at either transect and one ratio series from the Cook Plant data would fit in this general model category. Because the moving-average coefficient averaged approximately 0.85 for all data series examined, this coefficient was set equal to 0.85 for this set of simulations (see equation 6). A random number generator was used to generate a series of normally distributed error terms with mean zero and standard deviation of 1.6; 1.6 was within the range of standard deviations observed for ln (CP+1) or ln (RT+1) series. Results of increasing ϕ_1 on the degree of error in decision making were examined.

For each set of model parameters, 100 series were simulated. Each series comprised 70 observations (7 observations per year for 10 yr). For determining type I error, the first 35 observations were considered to be in the preoperational phase of the plant and the last 35 in the operational phase. An intervention analysis model (as described earlier, with step intervention beginning with the start of year 6) and an ANOVA model (same ANOVA model as described earlier) were then fitted to each of the 100 series. The significance level for all hypothesis testing was $\alpha = 0.05$. The significance of the step parameter, ω, in the intervention analysis model and the significance of the plant operation effect in the ANOVA were noted. The size of the type I error was determined for both statistical techniques. Because we set $\alpha = 0.05$, we would expect about 5 tests in 100 to show a significant difference between the operational phases of the plant, even though no difference was simulated. To determine if the type I error would change with a much larger variability in error, in two sets of simulations (sets of 100 generated series) the standard deviation of the error terms was set at 50.0.

Additionally, an undifferenced series was simulated of the form

$$(7) \quad Z_t = \phi_1 Z_{t-1} + \theta_m a_{t-m} + a_t$$

where Z_t = value of undifferenced series at time t, ϕ_1 = first-order autoregressive coefficient, θ_m = moving-average coefficient of order m, m = number of months in sampling year, a_t = residual at time t. We used this form in modeling two of the ratio series from the Cook Plant monitoring data. Again, a series of error terms with a normal distribution was produced with a random number generator; mean or the distribution was zero with a standard deviation of 0.65 (0.65 was the approximate standard deviation of the error terms of several ratio series). An undifferenced series of length 60 was generated. The first 30 observations were considered preoperational and the final 30 operational. The length of the generated series was chosen to be 60 to correspond with the length of the ratio series for gillnetted yellow perch adults from the Cook Plant monitoring study.

For investigating type II error, a step intervention, ω, was imposed on the latter half of observations when the series was generated. The number of tests with no significant ($\alpha = 0.05$) difference between preoperational and operational phases of the plant (incorrect decisions) was tallied for each set of 100 series corresponding to a particular set of model parameters. The first-order autoregressive coefficient, ϕ_1, and the step function, ω, were varied. For the undifferenced series, the

TABLE 1. Results of intervention analysis, ANOVA, and two-sample *t*-test applied to ratio (log plant-discharge abundance minus the log reference abundance) series for alewife and yellow perch monitoring data, D. C. Cook Plant, southeastern Lake Michigan, 1973–82. The step increase in the series with plant operation is ω, which is estimated via intervention analysis. The mean increase in the series is the operational mean value of the series minus the preoperational mean value of the series. AL = alewife, YP = yellow perch, m = number of months in sampling year. AR(1) denotes autoregressive of order 1 and MA(m) denotes moving average of order m. Asterisk denotes "white noise" series.

				Coefficients		Attained significance level of test for plant effect				
Species	Age group	Gear	Differencing?	MA(m)	AR(1)	t-test	ANOVA	Intervention analysis	Mean increase	ω
AL	Pooled	Trawl	Yes	0.8917	0	0.9751	0.9754	0.9998	−0.0123	0.0001
YP*	Pooled	Trawl	No	0	0	0.3498	0.3682	0.3498	−0.2699	−0.2699
AL	YOY	Trawl	No	0	−0.5286	0.6330	0.6433	0.0810	0.4803	−0.4170
YP*	YOY	Trawl	No	0	0	0.1258	0.1317	0.1258	−0.6596	−0.6596
AL*	Yearling	Trawl	No	0	0	0.9593	0.9595	0.9593	−0.0154	−0.0154
YP*	Yearling	Trawl	No	0	0	0.9996	0.9996	0.9996	0.0002	0.0002
AL*	Adult	Trawl	No	0	0	0.5670	0.5704	0.5670	0.1567	0.1567
YP*	Adult	Trawl	No	0	0	0.2940	0.3031	0.2940	−0.3073	−0.3073
AL	Pooled	Gill net	No	−0.3664	0	0.3943	0.3960	0.6407	0.2818	0.0858
YP	Pooled	Gill net	No	−0.4254	0.2689	0.0774	0.0824	0.6260	−0.5019	0.1042
AL	Adult	Gill net	No	−0.2877	0	0.3770	0.3850	0.5873	0.2948	0.0973
YP	Adult	Gill net	No	−0.4674	0.2604	0.0481	0.0531	0.6946	−0.5645	0.0851

moving-average coefficient of order m was also varied. Power of the test is equal to $1 - \beta$, where β is the size of the type II error.

In practice, often the preoperational and operational monitoring periods will not be equal. To investigate type I error for the type of unbalanced series applicable to the Cook Plant monitoring data, 10-yr series were generated with plant operation assumed to begin at the start of year 3. For type II error simulations for the unbalanced case, the intervention was imposed at the start of year 3.

The 95% confidence limits for type I and type II error were calculated by $p \pm 1.96\sqrt{p(1-p)/n}$ where p is the size of the type I or type II error calculated from the simulation of 100 series and n is the number of times the hypothesis was tested ($n = 100$) (Snedecor and Cochran 1980). The estimator is a large sample approximation to the confidence limits.

Note that sampling did not extend into winter months. In the trawl series, the October observation, although just prior to the April observation of the next year in the series, was separated from the April observation by 5 mo, while all other consecutive observations were 1 mo apart. A few simulations were performed to investigate the differences in time series structure between a series generated with 12 observations per year (1 observation each month) and a series of only April through October observations extracted from the 12 mo/yr series. The parent 12 mo/yr series was described by differencing of degree 12 and a moving-average term of order 12 (θ_{12} was set equal to 0.85). A first-order autoregressive term with coefficient equal to 0.4 was also included.

Results

Intervention Analysis and ANOVA of Monitoring Data

Of the 12 ratio series examined, 6 series could be considered "white noise"; that is, the observations could be considered independent of each other (Table 1). Three of the remaining six series showed a significant first-order autoregressive term; five of these six series exhibited a moving-average term of order m; m was the number of months per year in the series. The seasonality effect of the ratio series for yellow perch adults collected in gill nets exhibited the following pattern. In general, the ratio of log-abundances of plant and reference transects was positive in June and July, close to zero in August, and negative in September.

The application of intervention analysis, with the intervention beginning immediately in 1975, resulted in no significant interventions for any ratio series examined (Table 1). Application of ANOVA to the same ratio series disclosed no significant differences between phases of plant operation, although the test for plant effect for the ratio series of gillnetted yellow perch adults was close to significance (Table 1; Fig. 2). The month effect was not significant for this ANOVA application (as for all the other ratio series), and the two-sample t-test showed the operational series significantly less than the preoperational series.

Visual inspection of the ratio series gave no suggestion of any delayed responses except for a delayed-ramp response (beginning in 1978) for yellow perch yearlings collected in trawls (Fig. 3). This ramp response was significant (Table 2). The decline in the ratio was chiefly due to the decreasing ratio in the early months of the sampling year; when April and May were eliminated from the series, the delayed-ramp response was not significant. In gillnet samples, abundance of yellow perch adults during April and May was low compared with June through September; when April and May were dropped from the ratio series, plant effect was insignificant (t-test, $P = 0.8424$).

Trend Analysis

Series of log-abundance at plant-discharge and reference transects required differencing of degree m, with m equal to the number of months per year in the series. Furthermore, the model for these abundance series included a moving-average term of order m; estimates of the moving-average coefficient ranged from 0.84 to 0.96. Of the 24 log-abundance series at the transects (12 for the plant-discharge and 12 for the reference transect), 7 were modeled with a first-order autoregressive term. Other than the negative correlation coefficient for the

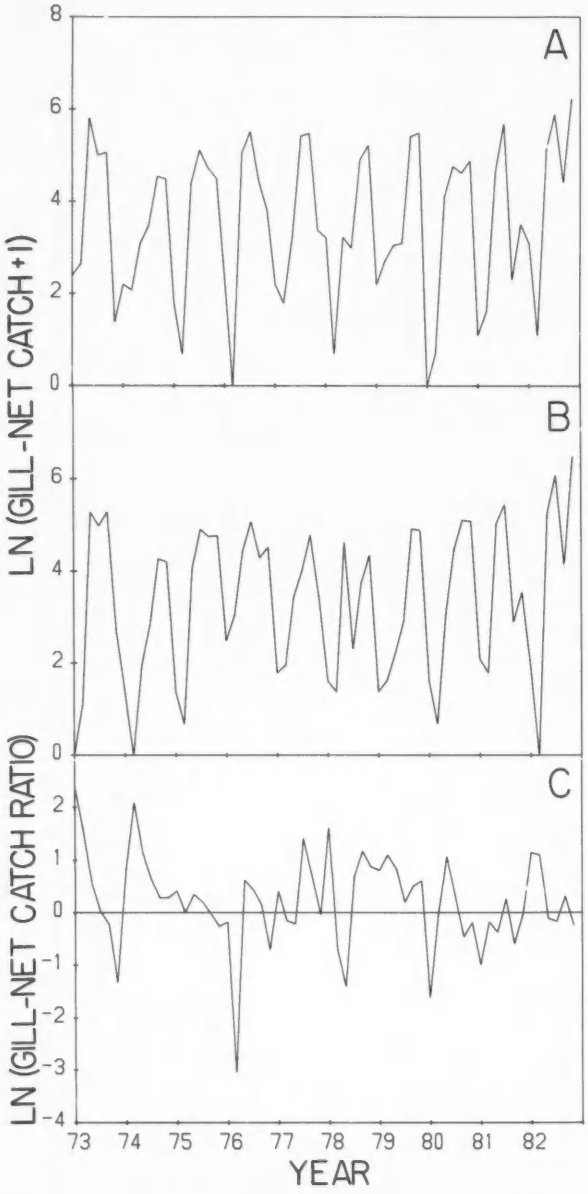

FIG. 2. Natural log(ln)-transformed catch (number of fish) at plant and reference transects and ln-transformed ratio of plant transect catch to reference transect catch of adult yellow perch collected in gill nets. Fish were caught near the D. C. Cook Plant, southeastern Lake Michigan, 1973–82. (A) Plant-discharge series; (B) reference transect series; (C) ratio series. Nonfishing months were ignored.

alewife YOY abundance series at the reference transect, all first-order autoregressive coefficient estimates ranged from 0.25 to 0.50.

Significant trends (of the ramp response) at both transects were detected for alewife adults caught in trawls and gill nets and for yellow perch YOY, yearlings, and adults caught in trawls (Table 3). For alewife, abundance decreased with time

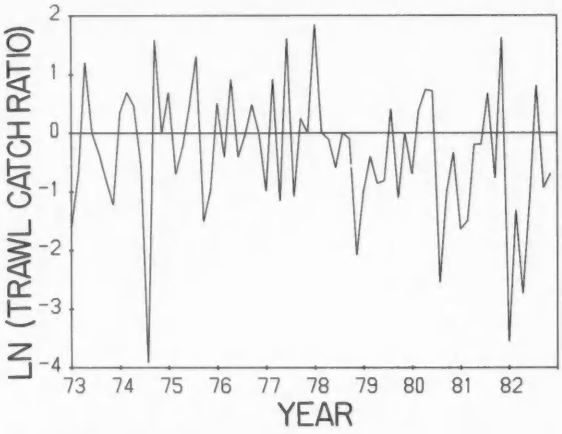

FIG. 3. Natural log(ln)-transformed catch (number of fish) ratio of plant transect catch to reference catch for yellow perch yearlings caught in trawls near the D. C. Cook Plant, southeastern Lake Michigan, 1973–82. Nonfishing months were ignored.

TABLE 2. Results of delayed-ramp response applied to the ratio series (difference in log abundance between plant and reference transects) of yearling yellow perch caught in trawls near the D. C. Cook Plant, southeastern Lake Michigan. The slope of the ramp response is ω. Standard error of the ramp slope is enclosed in parentheses. Ramp fitted for years 1978–82.

Months included in series	ω	Attained significance level
April–October	−0.2580 (0.06)	0.0016
June–October	−0.1303 (0.07)	0.0876

(negative slope) (Fig. 4), while the yellow perch abundance series showed a positive slope response. The abundance series for yellow perch adults collected in gill nets exhibited no significant trends.

Monte Carlo Simulation

The type I error of the ANOVA *F*-test for plant status effect increased as the first-order autoregressive coefficient increased from 0 to 0.8 (Table 4; Fig. 5). With a coefficient of 0.8, the type I error of the ANOVA *F*-test was 0.62; and with a coefficient of zero the error was 0.04, nearly identical to the 0.05 for the intervention analysis test for significance of ω. When a series was simulated in which differencing was unnecessary and the moving-average term was not included, but a first-order autoregressive term was ($\phi_1 = 0.4$), type I error results were similar to those for a series which required differencing and included a moving-average term (order equal to 7) and a first-order autoregressive term ($\phi_1 = 0.4$). Thus, results indicated that for the simulated series with a seasonal component described by differencing and a moving-average term close to 1 (0.85 in value), the autoregressive component was responsible for the inflated type I error in the ANOVA *F*-test.

Simulation results for the undifferenced series indicated that type I error of the ANOVA *F*-test increased with increasing ϕ_1. Furthermore, increasing the magnitude of θ_6 (from 0 to −0.5), coupled with a positive autoregressive component, led to a substantial increase in the type I error of the ANOVA pro-

TABLE 3. Significant trends in the ln-transformed catch (number of fish) at plant and reference transects for alewife and yellow perch. Fish were collected at the D. C. Cook Plant, southeastern Lake Michigan, 1973–82. Standard errors of transfer function parameters are enclosed in parentheses.

Species	Age group	Gear	Transect	Response	Transfer function parameters
Alewife	Pooled	Trawl	Plant	Ramp	$\omega = -0.21\,(0.08)$
Alewife	Pooled	Trawl	Reference	Ramp	$\omega = -0.23\,(0.09)$
Yellow perch	Pooled	Trawl	Plant	Ramp	$\omega = 0.26\,(0.07)$
Yellow perch	Pooled	Trawl	Reference	Ramp	$\omega = 0.34\,(0.07)$
Yellow perch	YOY	Trawl	Plant	Ramp	$\omega = 0.35\,(0.10)$
Yellow perch	YOY	Trawl	Reference	Ramp	$\omega = 0.40\,(0.10)$
Yellow perch	Yearling	Trawl	Plant	Ramp	$\omega = 0.21\,(0.07)$
Yellow perch	Yearling	Trawl	Reference	Ramp	$\omega = 0.29\,(0.06)$
Alewife	Adult	Trawl	Plant	Ramp	$\omega = -0.30\,(0.06)$
Alewife	Adult	Trawl	Reference	Ramp	$\omega = -0.31\,(0.07)$
Yellow perch	Adult	Trawl	Plant	Ramp	$\omega = 0.16\,(0.06)$
Yellow perch	Adult	Trawl	Reference	Ramp	$\omega = 0.20\,(0.07)$
Alewife	Pooled	Gill net	Plant	Ramp	$\omega = -0.18\,(0.04)$
Alewife	Pooled	Gill net	Reference	Ramp	$\omega = -0.22\,(0.05)$
Alewife	Adult	Gill net	Plant	Ramp	$\omega = -0.17\,(0.03)$
Alewife	Adult	Gill net	Reference	Ramp	$\omega = -0.23\,(0.05)$

TABLE 4. Size of type I error for test of significance of step intervention via intervention analysis and for ANOVA test. Error was estimated by Monte Carlo simulations. For each set of series parameters, 100 series were generated. Half-width of 95% confidence interval is enclosed in parentheses. m is the number of months per year of series generated. AR(1) denotes autoregressive of order 1 and MA(m) denotes moving average of order m. All differencing was of degree m. N = number of observations. Plant operation was assumed to begin at the start of year 6 of the 10-yr series, unless otherwise stated. An asterisk signifies that the operation was assumed to begin at the start of year 3 of the 10-yr series.

Series length (N)	Standard deviation of error term of series	Coefficients		Differencing?	Size of type I error	
		AR(1)	MA(m)		Intervention analysis	ANOVA
70	1.6	0.0	0.85	Yes	0.05 (0.04)	0.04 (0.04)
70	1.6	0.2	0.85	Yes	0.08 (0.05)	0.13 (0.07)
70	1.6	0.4	0.85	Yes	0.05 (0.04)	0.25 (0.08)
70	1.6	0.6	0.85	Yes	0.09 (0.06)	0.35 (0.09)
70	1.6	0.8	0.85	Yes	0.16 (0.07)	0.62 (0.10)
70	1.6	0.4	0.00	No	0.06 (0.05)	0.27 (0.09)
70*	1.6	0.4	0.85	Yes	0.09 (0.06)	0.21 (0.08)
70*	1.6	0.6	0.85	Yes	0.07 (0.05)	0.29 (0.09)
70*	1.6	0.8	0.85	Yes	0.11 (0.06)	0.55 (0.10)
70	50.0	0.4	0.85	Yes	0.06 (0.05)	0.26 (0.09)
70	50.0	0.8	0.85	Yes	0.05 (0.04)	0.58 (0.10)
60	0.65	0.0	−0.50	No	0.13 (0.07)	0.17 (0.07)
60	0.65	0.0	−0.80	No	0.09 (0.06)	0.16 (0.07)
60	0.65	0.25	0.00	No	0.10 (0.06)	0.13 (0.07)
60	0.65	0.25	−0.50	No	0.06 (0.05)	0.23 (0.08)
60	0.65	0.5	0.00	No	0.11 (0.06)	0.25 (0.08)
60	0.65	0.50	−0.50	No	0.11 (0.06)	0.45 (0.10)
60	0.65	0.50	−0.80	No	0.04 (0.04)	0.36 (0.09)
60*	0.65	0.25	−0.50	No	0.10 (0.06)	0.20 (0.08)

cedure (Table 4). Note that for $\theta_6 = 0$ and $\phi_1 = 0.5$ the type I error was 0.25, while for $\theta_6 = -0.5$ and $\phi_1 = 0.5$ the type I error was 0.45.

Simulation results for the type I error study were not sensitive to a wide range of error variability. Results were similar when the standard deviation of the error of the series was set at either 1.6 or 50 (Table 4).

Simulation of the differenced series showed that the ANOVA F-test was more powerful than the intervention analysis procedure, when the step intervention was 1.0, for all ϕ_1 from 0.2 to 0.6 (Table 5; Fig. 6). At ϕ_1 of 0.8, the difference in size of the type II error between the two statistical techniques had narrowed. Power of the ANOVA dropped rapidly when ϕ_1 increased from 0.6 to 0.8. When there was no autoregressive component of order one in the simulated model, the ANOVA was only slightly more powerful. For $\phi_1 = 0.4$, β was equal

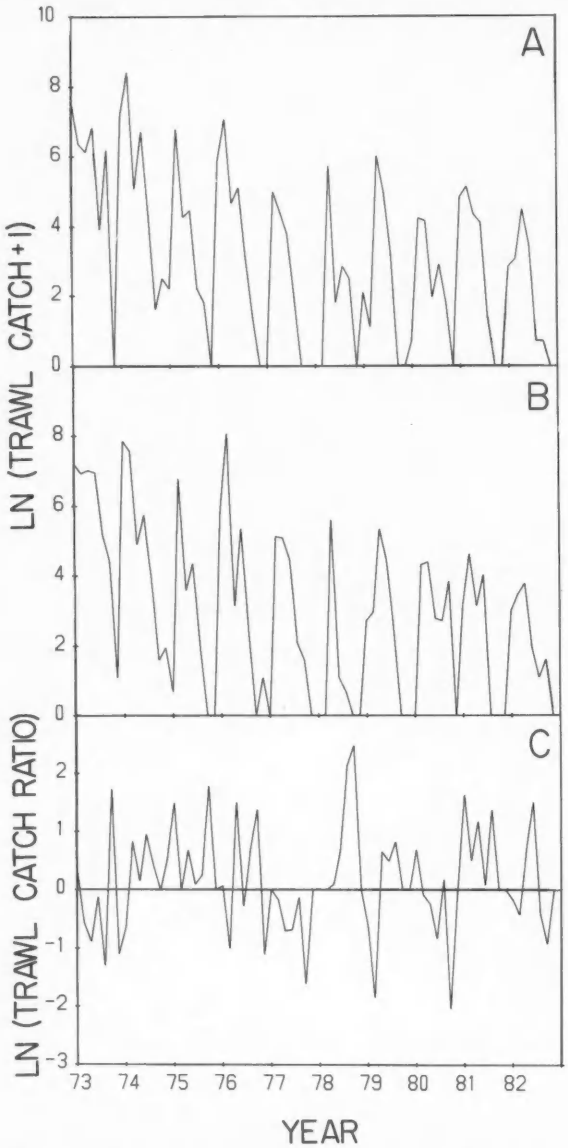

FIG. 4. Natural log(ln)-transformed catch (number of fish) at plant and reference transects and ln-transformed ratio of plant transect catch to reference transect catch of adult alewife collected in trawls. Fish were caught near the D. C. Cook Plant, southeastern Lake Michigan, 1973–82. (A) Plant-discharge series; (B) reference transect series; (C) ratio series. Nonfishing months were ignored.

to zero for a step intervention of 1.0 for the ANOVA *F*-test. However, β was not less than 0.05 until $\omega = 1.75$ for the intervention analysis test for significance of the step intervention.

For the undifferenced series, the ANOVA *F*-test was more powerful for $\phi_1 = 0.25$, $\theta_6 = -0.5$; β was zero for a step of 0.5 for the ANOVA *F*-test but β was zero for a step of 1.0 for the intervention analysis test of significance for ω. For a step intervention of $\omega = 0.4$ and $\theta_6 = -0.5$, power decreased for

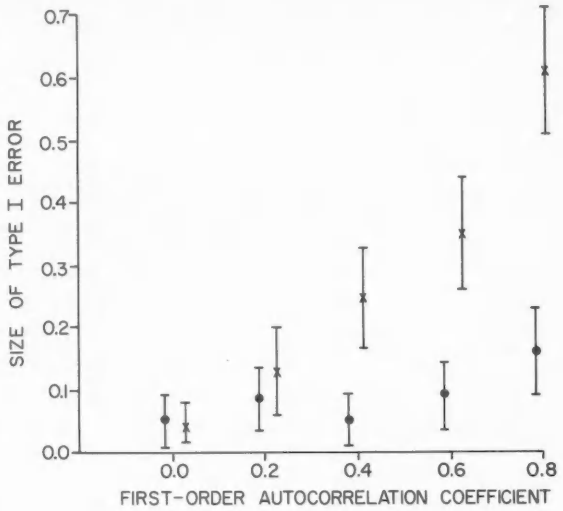

FIG. 5. Size of type I error as a function of the first-order autoregressive coefficient, ϕ_1. Based on Monte Carlo simulations (100 trials for each value of ϕ_1) for a differenced series with moving-average coefficient (order 7) equal to 0.85. ×, result for ANOVA; ●, result for intervention analysis; 95% confidence intervals are included. Plant operation was assumed to begin at the start of year 6 of the 10-yr series.

both intervention analysis and ANOVA hypothesis testing as the ϕ_1 was increased from 0 to 0.5 (Table 5).

The unbalanced series (2 yr preoperational, 8 yr operational) simulations suggested that type I error was slightly more inflated in the balanced (5 yr preoperational, 5 yr operational) ANOVA compared with the unbalanced ANOVA (Table 4). Both intervention analysis and ANOVA were more powerful in the balanced series rather than the unbalanced series (Table 5). The same general patterns in type I and type II error observed for the balanced series were found for the unbalanced series.

The simulation results of the 7 mo/yr series extracted from a 12 mo/yr series showed that the two series were similar in time series structure. Both these series required differencing, and the estimates of the moving-average coefficients for the seasonality component were not significantly different between the two series (as determined by a *t*-test for paired comparison, with $\alpha = 0.05$). The first-order autoregressive coefficient estimated for the 7 mo/yr series was less than the estimated ϕ_1 for the parent series (as determined by a *t*-test for paired comparison for the 100 pairs of series simulated). For the parent series, the mean ϕ_1 was equal to 0.39 and for the extracted series the mean ϕ_1 was 0.31. These results supported the contention that series with observations missing from the same winter months for each year of the series observations may be analyzed via intervention analysis without serious problems.

Discussion

Intervention analysis and ANOVA applied to the Cook Plant monitoring data indicated that the power plant had no effect on alewife and yellow perch abundances during summer. Observations from months of relatively low abundance (such as April and May for yellow perch in the plant vicinity) strongly influenced the outcome of hypothesis testing for either technique.

TABLE 5. Size of type II error for test of significance of step intervention via intervention analysis and for ANOVA test. Error was estimated by Monte Carlo simulations. For each set of series parameters, 100 series were generated. Step intervention, ω, was imposed on each series at start of year 6 of the 10-yr series, unless otherwise stated. Half-width of 95% confidence interval is enclosed in parentheses. m is the number of months per year of series generated. AR(1) denotes autoregressive of order 1 and MA(m) denotes moving average of order m. All differencing was of degree m. N = number of observations. An asterisk signifies that step intervention was imposed on the series at the start of year 3 of the 10-yr series.

Series length (N)	Standard deviation of series error term	Coefficients				Size of type II error	
		ω	AR(1)	MA(m)	Differencing?	Intervention analysis	ANOVA
70	1.6	1.00	0.0	0.85	Yes	0.00 (0.00)	0.00 (0.00)
70	1.6	1.00	0.2	0.85	Yes	0.27 (0.09)	0.00 (0.00)
70	1.6	1.00	0.4	0.85	Yes	0.71 (0.09)	0.00 (0.00)
70	1.6	1.00	0.6	0.85	Yes	0.90 (0.06)	0.16 (0.07)
70	1.6	1.00	0.8	0.85	Yes	0.89 (0.06)	0.73 (0.09)
70	1.6	0.75	0.4	0.85	Yes	0.96 (0.04)	0.51 (0.10)
70	1.6	1.25	0.4	0.85	Yes	0.30 (0.09)	0.00 (0.00)
70	1.6	1.50	0.4	0.85	Yes	0.09 (0.06)	0.00 (0.00)
70	1.6	1.75	0.4	0.85	Yes	0.03 (0.03)	0.00 (0.00)
70	1.6	0.90	0.0	0.85	Yes	0.04 (0.04)	0.01 (0.02)
70	1.6	0.80	0.0	0.85	Yes	0.13 (0.07)	0.10 (0.06)
70*	1.6	1.0	0.4	0.85	Yes	0.94 (0.05)	0.45 (0.10)
70*	1.6	1.0	0.6	0.85	Yes	0.93 (0.05)	0.73 (0.09)
70*	1.6	1.25	0.4	0.85	Yes	0.66 (0.09)	0.00 (0.00)
60	0.65	0.40	0.25	−0.50	No	0.48 (0.10)	0.20 (0.08)
60	0.65	0.50	0.25	−0.50	No	0.41 (0.10)	0.00 (0.00)
60	0.65	0.75	0.25	−0.50	No	0.13 (0.07)	0.00 (0.00)
60	0.65	1.00	0.25	−0.50	No	0.00 (0.00)	0.00 (0.00)
60	0.65	0.40	0.50	−0.50	No	0.66 (0.09)	0.46 (0.10)
60	0.65	0.50	0.50	−0.50	No	0.51 (0.10)	0.04 (0.04)
60	0.65	0.75	0.50	−0.50	No	0.29 (0.09)	0.00 (0.00)
60	0.65	0.40	0.00	−0.50	No	0.32 (0.09)	0.13 (0.07)
60	0.65	0.40	0.50	0.00	No	0.51 (0.10)	0.37 (0.09)
60*	0.65	0.50	0.50	−0.50	No	0.51 (0.10)	0.45 (0.10)

For example, consider yellow perch yearlings in the Cook Plant vicinity. Yellow perch are widely dispersed in the lake during their first winter but move toward shallower water (9 m or shallower) in spring. However, yearling yellow perch trawl catch in the study area does not peak until summer or early fall (Jude et al. 1975, 1979). The delayed-ramp response in the ratio series (series generated by subtracting log abundance at the reference transect from log abundance at the plant-discharge transect) mainly represented a change in the April and May catches which occurred from 1978 through 1982. During this period the pattern of more yellow perch yearlings arriving within the 9-m contour at the reference transect than at the plant transect became more pronounced. This pattern was not observed during peak abundance months.

April and May data had a substantial effect on the ANOVA of the ratio series for gillnetted yellow perch adults. Jude et al. (1979) and Tesar et al. (1985) found that yellow perch adults, particularly those collected in gill nets, did not occur in substantial abundances in the sampling areas until summer. The significant difference detected by the two-sample t-test between the preoperational and operational periods was largely due to a pattern in April and May catches which was related to operation of the power plant. Before the plant began operation, catch was usually greater at the plant-discharge transect than at the reference transect during April and May; however, when the plant was operating, catch was usually greater at the reference rather than the plant transect during these 2 mo. As far as the peak abundance months (summer) were concerned, no changes in the catch ratio attributable to plant operation were detected.

Results of statistical testing showed that the Cook Plant had no effect on alewife abundance throughout the sampling year (not just the summer months). The alewife is pelagic, while the yellow perch is benthic; yellow perch feed on benthic invertebrates and usually deposit their eggs on the lake bottom. A limestone riprap bed was placed beneath and around the intake and discharge structures of the Cook Plant to provide support. With time, silt and sand settled on parts of the riprap; perhaps this settling rendered the plant-discharge transect less attractive to yellow perch yearlings and adults during the spring months than the transect had been. Perhaps ecological succession of the benthic invertebrates on the riprap (see Rutecki et al. 1985) had occurred, such that within a few years the plant-discharge transect was not as attractive to yellow perch during the spring months as the transect once was.

Serial correlation (lack of independence among observations such that each observation is dependent on a set of previous observations) in monitoring data should be considered when evaluating power plant impact on fish populations. Intervention analysis explicitly accounts for serial correlation, whereas one of the assumptions of ANOVA is independence among observations. The nature and magnitude of autocorrelation in the

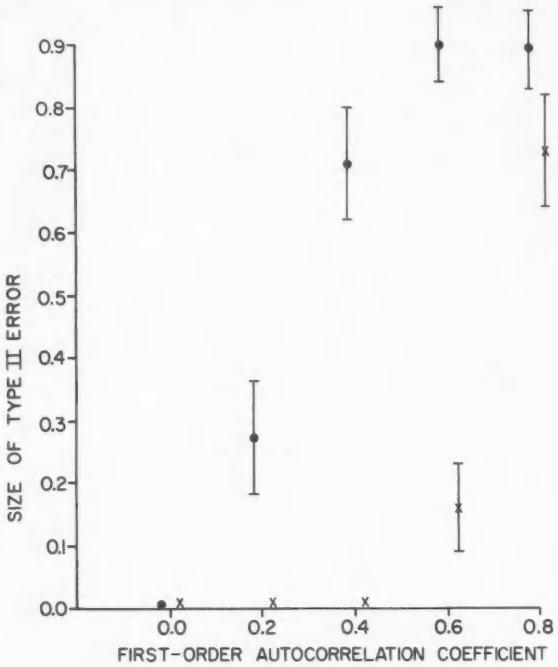

FIG. 6. Size of type II error as a function of the first-order autoregressive coefficient ϕ_1. Based on Monte Carlo simulations (100 trials for each value of ϕ_1) for a differenced series with moving-average coefficient (order 7) equal to 0.85. Step intervention of $\omega = 1.0$ imposed at halfway point of the series (start of year 6 of the 10-yr series). ×, result for ANOVA; ●, result for intervention analysis; 95% confidence intervals are included.

data affect the relative performance of intervention analysis and ANOVA in detecting change in fish abundance with power plant operation.

Many ratio series for the Cook Plant data were considered "white noise"; that is, observations were independent of each other. In such cases, the "general" intervention model (equation 3) for a step intervention was reduced to a two-sample *t*-test model because the autoregressive and seasonality components were not present. Some ratio series exhibited autocorrelations such that the type I error of ANOVA was inflated. However, for these same cases of autocorrelation, ANOVA was a more powerful technique (better able to detect changes in the ratio series with plant operation) than intervention analysis.

A seasonal effect in the ratio series on fish abundance was present whenever there was an interaction effect between season and transect. For example, consider gillnetted yellow perch adults. The first-order autoregressive (AR(1)) component is often present in a wide variety of environmental monitoring series. Saila et al. (1980) used this component in modeling a 12-yr time series of monthly catch of rock lobster (*Jasus edwardsii*) from New Zealand. The AR(1) component was present in several abundance series for the reference and plant-discharge transects, but was infrequently observed in the Cook Plant ratio series. The time series that lacked the AR(1) component frequently showed relatively sharp increases or decreases between adjoining observations, particularly between the last observation of one year and the first observation of the next year. The abundance and ratio series for the Cook Plant lacked correlation between abundances (or ratios of abundance) separated in time by duration of one reproductive cycle (duration of reproductive cycle was 2−3 yr for yellow perch and alewife in the plant vicinity). This result agreed with the finding of Madenjian (1979), who concluded, after applying time series analysis to a variety of commercial fisheries, that usually a relatively high catch one year did not imply high catch one reproductive cycle later.

When ANOVA (or two-sample *t*-test) indicates a significant change in the ratio series with plant operation, while intervention analysis shows no plant effect, two explanations are feasible. The intervention analysis may have failed to detect a true change in the ratio series with power plant operation, or ANOVA may have detected a difference in the ratio series between preoperational and operational phases when no such difference existed. There is no sure way of knowing which alternative is correct. Whenever either technique detects a significant plant effect, the effect of months of relatively low abundance should be investigated.

The trend analysis of the reference and plant-discharge log-abundance series corroborated the suspected lakewide trends. The alewife population had been fluctuating throughout Lake Michigan from 1967 to 1978 (Hatch et al. 1981), with a decline in recent years (Wells and Hatch 1984; Jude and Tesar 1985). Our trend analysis showed a significant decline in abundance at both transects for adult alewife. The significant trends at both transects for the yellow perch trawl series (YOY, yearling, and adult) were chiefly due to large year classes in 1980−82, the large yearling catch in 1981, and the large adult catch in 1982. Indeed, the recent (early 1980's) abundance of yellow perch in Lake Michigan is believed to be at the highest level of the past 25 yr (Wells and Hatch 1984). Our trend analysis results provided a rigorous demonstration of the recent alewife decline and yellow perch increase in Lake Michigan. Unlike the series for yellow perch adults caught in trawls, the plant or reference series for adult yellow perch captured in gill nets showed no significant trends. Jude et al. (1975) observed that gill nets were more efficient at catching larger yellow perch adults than trawls, which may explain the difference in trends between the series based on the two different gear.

Based on the study of type I error and type II error for the ANOVA and intervention analysis procedures, neither procedure is superior overall. For impact assessment, the series determined by the difference in log (abundance + 1) between the power plant and reference transects should be examined. When the log difference series exhibits serial correlation, we recommend application of both techniques. If both techniques detect a significant difference in the ratio between the two phases of plant operation, the result of the intervention analysis will confirm that the difference indicated by the ANOVA was not the result of a type I error due to autocorrelation in the ratio series. Impact assessment based solely on ANOVA, even when the ratio series exhibits significant serial correlation, could result in type I error, that is, concluding that a change had occurred in the ratio series with plant operation when actually no change had taken place. When a significant difference is detected via either technique, it should be ascertained whether observations from months of relatively low abundance contributed substantially to the significant difference.

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Interaction between Pacific Cod (*Gadus macrocephalus*) and Herring (*Clupea harengus pallasi*) in the Hecate Strait, British Columbia

Carl J. Walters

Institute of Animal Resource Ecology, University of British Columbia, Vancouver, B.C. V6T 1W5

and M. Stocker, A. V. Tyler, and S. J. Westrheim

Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6

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Pacific cod (*Gadus macrocephalus*) and herring (*Clupea harengus pallasi*) in the Hecate Strait have shown fluctuations consistent with the hypothesis that herring recruitment rates are strongly influenced by cod predation. Regression analyses of herring juvenile survival, as measured by log recruits per herring spawner, on Pacific cod abundance indicate that the cod may cause a total instantaneous mortality rate averaging around $0.75 \cdot yr^{-1}$ with each cod consuming several hundred herring. Somewhat lower estimates of herring consumption per cod were expected on the basis of stomach contents data, but the discrepancy may well be due to systematic underestimates of cod abundance. Cod recruitment rates are positively correlated with herring abundance, but it is impossible to determine from historical data whether this correlation reflects predator–prey interdependence or the impacts of older cod on their own offspring, since cod and herring abundances are inversely correlated. Peak cod abundances in northern British Columbia during the late 1950's may be partly responsible for the collapse of the herring reduction fishery of the 1960's, and management of the two species should be coordinated to reflect the possibility of similar events in the future.

Il y a eu fluctuation des populations de morue du Pacifique (*Gadus macrocephalus*) et du hareng (*Clupea harengus pallasi*), dans le détroit d'Hecate, en accord avec l'hypothèse voulant que la prédation par la morue influe grandement sur les taux de recrutement du hareng. Les analyses de régression de la survie des jeunes harengs, telle que mesurée d'après les recrues à l'échelle logarithmique par hareng reproducteur, sur l'abondance de morue du Pacifique montrent que la morue peut provoquer un taux total de mortalité instantanée s'élevant en moyenne à environ $0{,}75 \cdot an^{-1}$, chaque morue consommant plusieurs centaines de hareng. On s'attendait, d'après les données des contenus stomacaux, à des estimations un peu plus faibles, mais la divergence peut très bien être attribuable à des sous-estimations systématiques de l'abondance des morues. Il y a une corrélation positive entre les taux de recrutement des morues et l'abondance des harengs, mais il est impossible de déterminer à partir des données antérieures si cette corrélation reflète l'interdépendance entre le prédateur et la proie ou les répercussions de morues plus âgées sur leur propre progéniture, étant donné qu'il y a une corrélation inverse entre le nombre de morues et le nombre de harengs. Les pics d'abondance des morues observés dans le nord de la Colombie-Britannique à la fin des années 50 peuvent être en partie responsables de l'effondrement de la pêche du hareng pour transformation en farine pendant les années 60, et la gestion des deux espèces doit être coordonnée pour tenir compte de la possibilité que des événements semblables se reproduisent dans l'avenir.

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Species interactions involving predation are a major topic of discussion in fisheries, but it has been difficult to demonstrate the importance of such interactions as causes of variation in recruitment and survival rates. The presence of individuals of one species in the guts of another does not imply that the predation will cause changes in aggregate recruitment–mortality rates in the prey population, since the predator may select individuals that would soon die anyway; likewise, aggregate rates in the predator population may not respond to changes in the abundance of one prey species, since the predators may still have no difficulty in capturing enough of the same or alternative prey. Therefore, it is necessary to demonstrate empirically that aggregate recruitment–mortality rates in the interacting species do change as their abundances change, and to demonstrate that the rate changes are not due to some external factor that has an opposite influence on the species (e.g. enhance predator survival while reducing prey survival). The role of external factors cannot be determined unambiguously unless controlled experiments are carried out to deliberately establish contrasting prey–predator abundance combinations. Such large scale experiments have not been conducted in marine systems, so at present we can only determine whether the recruitment–survival correlations predicted by predation theory are present in historical time series. The purpose of this paper is to show that recruitment rates for Pacific cod (*Gadus macrocephalus*) and herring (*Clupea harengus*

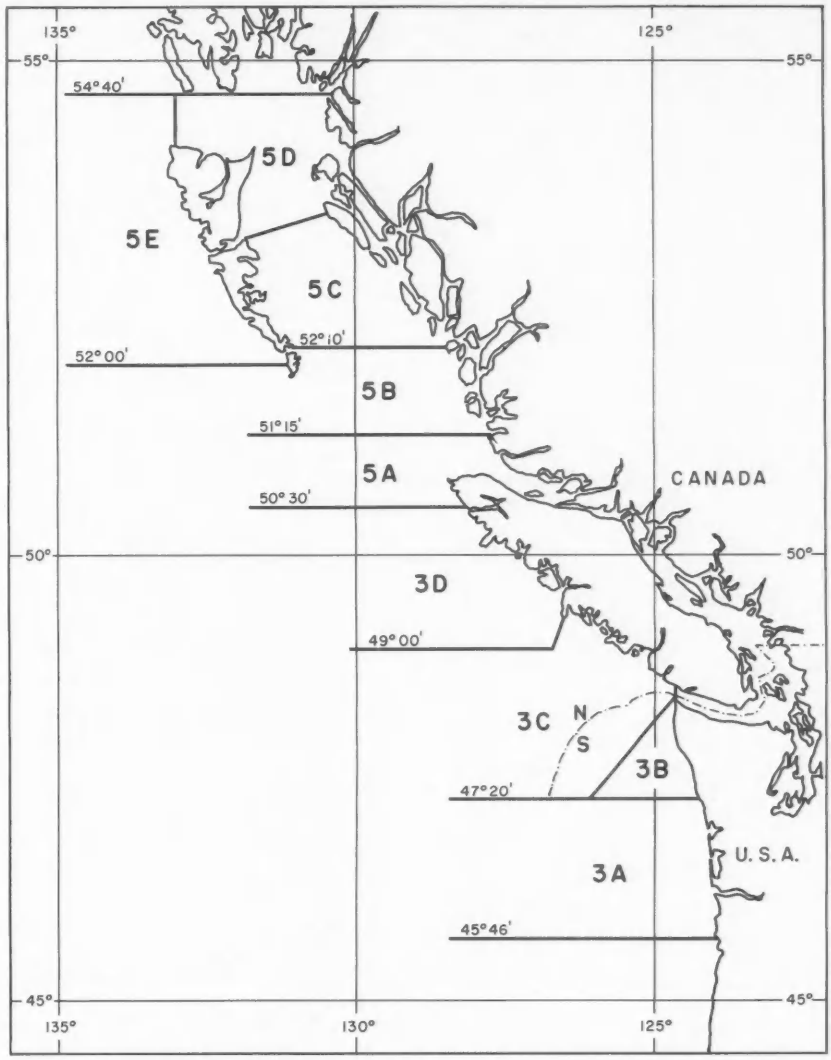

FIG. 1. Location of the Hecate Strait and other statistical areas off the British Columbia coast.

pallasi) in the Hecate Strait have fluctuated in a pattern consistent with simple predation models.

The analyses presented here were conducted as part of a 1984 workshop aimed at developing ecosystem models of the Hecate Strait (Tyler et al. 1986). During that workshop, participants assembled a microcomputer data base of time series data for 1955–75 on catches and abundance estimates for a variety of fish species and several physical variables such as sea surface temperatures and Ekman transport rates. Based on spatial distribution and stomach contents data, a number of potentially important predator–prey linkages were identified, including that of cod and herring. It was further noted that cod and herring are among the most abundant species in the Strait. Other abundant piscivores besides cod are Pacific salmon (*Oncorhynchus* spp.), spiny dogfish (*Squalus acanthias*), rock sole (*Lepidopsetta bilineata*), and sablefish (*Anoplopoma fimbria*). The most abundant alternative prey fish besides herring is the sandlance (*Ammodytes hexapterus*). Cod and herring stocks fluctuated greatly over the 1955–75 period, and cod stomach samples indicate that sandlance abundance may also have fluctuated markedly (Westrheim and Harling 1983). Crude, preliminary estimates of abundance and feeding rates were made for the various piscivores and these estimates led us to look more closely at the cod–herring interaction; most other predator–prey linkages appear to be quantitatively much less important, and time series data involving contrasting abundances were not available for most of them.

Data Sources and Estimation Procedure

For statistical purposes, we defined Hecate Strait as comprising International Statistical Areas 5C and 5D (Fig. 1). The trawl fishery there for Pacific cod (≥ age 2) varies temporally and spatially (Westrheim and Tagart 1984; Tyler and

McFarlane 1985; Westrheim and Foucher 1985). During April–September most of the cod are caught in relatively shallow water (18–108 m), principally in northern 5D and central 5C; landings during October– December are minimal. During January–March, cod congregate for spawning at 50–69 fth (92–126 m) in southeast 5D and to a lesser extent in west-central 5C. The complete distributions of juvenile and adult cod are not known, but juveniles (age 0–2) are often found in catches of adult cod.

The temporal and spatial distribution of herring in Hecate Strait is not fully known. Adult herring concentrate during January–March in the same areas as cod, but spawn in the nearby inlets. However, the herring stocks spawning in inlets adjacent to Hecate Strait do not necessarily reside in Hecate Strait for the rest of the year. The major migratory herring populations that spawn in inlets surrounding the Strait, and that are thought to reside in the Strait, are (1) the Queen Charlotte Islands stock grouping, (2) the North Coast stock grouping, and (3) the Central Coast stock grouping (Haist and Stocker 1984). The latter stock grouping spawns along the mainland coast but may stray into Hecate Strait. Because the Central Coast stock grouping is in phase with the combined stocks to the north, these three populations were combined to form a major north coast stock complex. It was at this level of aggregation that stock reconstruction was carried out for the analysis presented below.

Stomach contents samples for cod were collected routinely over the 1955–75 study period (Westrheim 1977; Westrheim and Harling 1983). These samples indicate that cod feed on herring mainly in the winter months, January–March, when there is an average of six to eight herring per cod stomach representing about 30% of the cod diet by weight. Herring of all sizes are taken. Stomach samples taken from cod landed commercially indicate that fish age 2 and older are eaten, although very large herring are not found (D. Hay, Pacific Biological Station, Nanaimo, B.C., unpubl. data). While herring are found in the guts of smaller cod, the main predation appears to be by mature, spawning cod (≥ age 3). Assuming that cod stomachs turn over about once every other day during January–March, the above information implies that mature cod each eat around 420 herring per year. These cod grow around 1 $kg \cdot yr^{-1}$; assuming that they have a growth efficiency of around 20%, that (0.25) × (0.3) of this growth is due to feeding on herring in winter, and that the herring consumed average around 12 g each, a lower estimate would be around 75 herring per mature cod per year. We present these estimates only to indicate that stomach contents data imply that the annual herring consumption per cod is in the neighborhood of one to a few hundred, if Pacific cod are anything like Atlantic cod (*Gadus morhua*) in feeding and digestion rates (Jones 1979; Durbin et al. 1983).

Extensive age composition data have been gathered from landings of cod and herring stocks as defined above. Cod have been aged mainly by length frequency analysis, and the data are summarized in Foucher and Westrheim (1984) and Westrheim and Foucher (1985). Herring age compositions have been determined mainly by scale analysis, and the estimates used here are from corrected summaries prepared by V. Haist (Pacific Biological Station, Nanaimo, B.C., pers. comm.) using data extracted from Hourston and Nash (1972) and Hourston (1981).

Recruitment rates and stock sizes at age for 1955–75 have been estimated from the age composition data using cohort analysis for cod (Walters et al. 1982) and the more sophisticated maximum likelihood procedure of Fournier and Archibald (1982) as modified for herring by Stocker et al. (1983). The VPA and Fournier procedures give qualitatively similar recruitment patterns over time. Our analysis for herring was based on the Fournier procedure, assuming a constant natural mortality rate of 0.45 for older fish, and using spawn survey as well as catch at age data (Haist and Stocker 1984). We decided to base our analyses for cod on VPA estimates following the procedures of Walters et al. (1982) rather than Fournier (1983); the VPA estimates use updated age composition data not available when Fournier did his analysis, are more conservative (lower) than his estimates, and indicate more variable recruitment rates over time. For our analyses, the major difficulty with these estimates is that the variation in cohort strengths over time has probably been underestimated, due to "smearing" of sampled fish across cohorts by ageing errors. This difficulty may be particularly severe for the cod data (Westrheim and Foucher 1985, p. 100).

The numbers of adult (≥ age 3) cod and adult (≥ age 3) herring were taken as indices of spawning stock each year, and were multiplied by an average effective fecundity (2000 and 1000 for herring and cod, respectively) to give an annual larval production estimate, E_t. The effective fecundity of 2000 for herring represents approximately 10% of the average total fecundity, and hence allows for substantial prehatching and early larval mortality (the precise levels of these losses are not critical to our analyses); annual average fecundities were not estimated from age–size composition data, since the average sizes at age and percentage age compositions did not vary significantly over the time period studied here (Ware 1985; Hourston 1981; Hourston and Nash 1972). We then took $Z_t = \log$ (recruits/eggs) as indices of the recruitment success of each stock in each stock in year t. According to standard Ricker stock–recruitment theory, intraspecific competition and cannibalism should result approximately in the linear relationship

$$(1) \quad Z_t = a - bE_t + W_t$$

where a is a background, density-independent mortality rate, bE_t represents additional density-dependent mortality due to intraspecific competition or possibly cannibalism, and W_t is a random mortality component due to abiotic factors and biotic factors not closely correlated with stock size as measured by E_t. We employed a simple extention of equation (1) to account for species interactions, with the linear relationship

$$(2) \quad Z_t = a - bE_t \pm qP_t + W_t$$

where P_t is the number of predators (for herring Z_t predictions) or prey (for cod Z_t predictions). The parameter q should be negative if P_t is the number of predators, and is interpreted as the fraction of the prey stock taken by each predator prior to prey recruitment. The value of q should be positive if P_t is the prey stock, and represents the effect of increasing prey abundance on predator fecundity and/or juvenile survival; enhanced survival might occur for example if the predator cannibalizes fewer of its own young when the prey species is more abundant. Equation (2) is the functional form used to represent species interactions in the Anderson and Ursin (1977) and Sheperd (1984) models, and has been recommended (Doyle, p. 47 in May 1984) as a framework for exploratory data analysis of possible species interactions using multiple regression techniques. Obviously, equation (2) can be generalized to include a whole series of terms for different predators and alternative prey species.

Equation (2) makes two key assumptions when applied to the Z_t time series for a prey species such as herring. First, it proposes that predation loss (as represented by P_t) is independent of loss due to intraspecific interactions (represented by bE_t) such as food competition. If, for example, increased juvenile density results in more juveniles with poor growth and these individuals are subject to higher predation losses, such losses will be reflected in the b coefficient rather than the predation coefficient q. Second, it proposes that the predator's individual functional response to prey density is linear, i.e. (captures per predator) = q (prey available), thus ignoring effects of predator handling time and satiation when prey density is high. If the predator attacks a variety of prey species $j = 1, \ldots, n$ at random, where the prey densities are N_j, rates of effective search are a_j, and handling times per prey are h_j, then the attack rate per predator C_i on any prey species i would be more realistically represented by the multispecies disc equation (Murdoch 1973; Walters 1985a):

$$(3)\quad C_i = \frac{a_i N_i}{1 + \sum_j a_j h_j N_j} = \frac{a_i N_i}{1 + a_i h_i N_i + B}$$

where $B = \sum_{j \neq i} a_j h_j N_j$ represents the effect of alternative prey on the rate for species i. The total instantaneous mortality rate on species i would be given by

$$(4)\quad C_i P_t / N_i = a_i P_t / (1 + a_i h_i N_i + B).$$

In pretending that this mortality rate is adequately represented by qP_t, equation (2) assumes that h_i is negligible (satiation on prey i rare) and that the densities of alternative prey are relatively constant (so that $q \approx a_i/(1 + B)$ is a constant). In principle we could substitute equation (4) into equation (2) to give a nonlinear regression model for predation effects, but Monte Carlo simulation tests of that approach (using fake data with known parameters) indicated that poor convergence and estimates could be expected from nonlinear estimations for data sets such as the Hecate Strait herring and cod.

A few further words of caution are needed about using equation (2) as a regression model to estimate the importance of species interactions. First, the regression independent variables E_t and P_t are estimated with both random error and systematic (autocorrelated) error due to misageing of fish. Such errors will tend to cause b to be overestimated (Walters and Ludwig 1981), and may cause q to be underestimated (make Z appear to be independent of P_t). Second, the E_t and P_t are not designed independent variables, but are instead random variables that are correlated with past values of the random effects W_t. Such correlations may exaggerate the biases due to measurement errors (Goodyear and Christensen 1984, Walters 1985b). Third, there may be correlation between environmental factors (whose effects are supposedly measured by W_t) and the space–time pattern of contact between prey and predators, so that q is in fact time varying and correlated with W_t; such correlations may either exaggerate or mask the apparent predation effects as measured by qP_t where q is the (constant) estimate from regression analysis. Fourth, there is hidden ambiguity in equation (2) about when the prey are actually eaten. Z_t is assumed to be a mortality prior to recruitment, but is calculated from estimated recruitment which in turn is estimated from catches 3–10 yr later; thus, predation mortality occurring any-

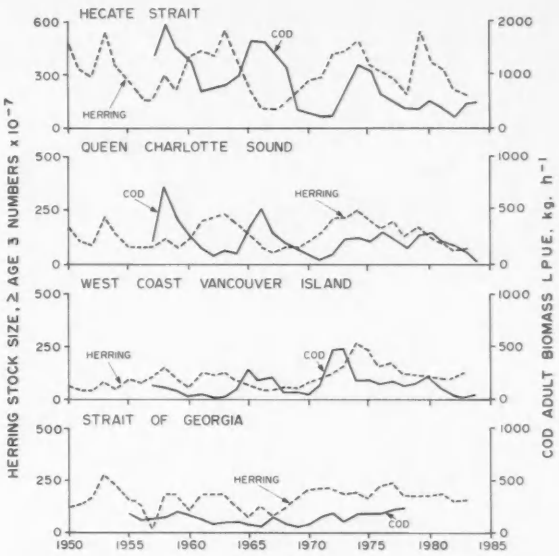

FIG. 2. Estimates of adult herring stock size compared with adult cod stock size (landings per unit effort) for various regions of the British Columbia coast, from data in Haist and Stocker (1984) and Westrheim and Foucher (1985). Cod catch regions are as named. Hecate Strait (Areas 5C–5D) herring include Queen Charlottes and North Coast stocks, Queen Charlotte Sound (Areas 5A–5B) herring are central coast stock, West Coast Vancouver Island (Areas 3C–3D) and Georgia Strait plus Johnstone Strait (Area 4B) stocks are as reported in Haist and Stocker (1984).

where in the prey life cycle (years $t + 1$, $t + 2$, etc.) and influencing the cohort catches will also influence the recruitment estimate, provided the recruitment estimate was obtained with a model assuming constant natural mortality. Finally, and perhaps most important, we examined many time series before noticing the correlations presented here; such examinations are likely to uncover correlations that are due to chance alone, and we were unable to quantify this risk since no record was kept of the number of time series examined.

Results

A general indication on the possible importance of the cod–herring interaction of the British Columbia coast is provided by Fig. 2, where we compare Haist and Stocker (1984) estimates for herring adult (≥ age 3) stock size to the cod landings per unit effort (LPUE) reported in Westrheim and Foucher (1985) for four major regions. The pattern for Hecate Strait is reminiscent of a predator–prey cycle where years of high herring abundance are followed by strong cod catches and strong cod catches are followed by low herring abundance.

Egg deposition and recruitment estimates for Hecate Strait cod and herring as defined above are presented in Table 1. Linear regression of Z_t calculated from Table 1 on E_t and P_t, as defined in equations (1) and (2), gave reasonable estimates for the b and q parameters (Table 2). The sign of the q parameters was as predicted by predation theory: increases in cod abundance apparently have a negative effect on herring juvenile survival, while increases in herring abundance have a positive effect on cod recruitment. Standard measures of statistical

TABLE 1. Stock and recruitment data assumed for cod and herring. Herring effective egg deposition E_t was taken as column (1) × 2000. Cod effective egg deposition E_t was taken as column (3) × 1000. All numbers are millions of fish.

Year	Herring adult (≥ age 3) stock size (1)	Herring age 1 recruits, year $t+1$ (2)	Cod adult (≥ age 3) stock size (3)	Cod age 1 recruits, year $t+1$ (4)
1955	2640	3590	1.9	2.1
1956	1720	5860	1.1	4.3
1957	1820	1820	1.9	4.3
1958	3120	7560	3.7	2.1
1959	2140	6270	3.7	2.8
1960	4070	5140	1.9	4.3
1961	4350	9680	1.8	6.9
1962	4210	3550	2.5	7.8
1963	5610	1280	3.8	4.4
1964	4030	670	6	3.2
1965	2320	1970	6.6	4.2
1966	1170	2140	5.1	1.4
1967	1050	2700	3	1.7
1968	1470	3430	2.6	2.4
1969	2030	3290	1.5	3.1
1970	2650	6080	1.3	4.6
1971	2940	4440	2.1	3.4
1972	4240	5500	3	4
1973	4370	1690	3.9	3.3
1974	4890	2540	3.3	3.1
1975	3670	2100	3	3.4

significance for the parameter estimates are not presented; such measures would be misleading in view of the correlation patterns that are likely present in the data, and in view of the unknown risk that we stumbled upon a spurious correlation after examining many data series.

Figures 3 and 4 compare fits to the recruitment time series for equation (1) versus equation (2). It is obvious that the standard Ricker stock–recruitment relationships (equation (1)) cannot account for much of the observed fluctuations in recruitment rates, especially for herring. By including the effects of cod predation, we can account for much of the decline and recovery in herring recruitment rates that followed the peak herring recruitment years of 1958–60. However, these peak years are not fully accounted for by the model, nor is the peak in cod recruitment that followed in 1961–62 (age 2 recruits in 1963–64). It is a trivial matter to simulate the dynamics implied by equations (2.3) and (2.4) in Table 2; using reasonable estimates of annual survival rates (0.5–0.6 for both species), such simulations indicate damping oscillations to a predator–prey equilibrium. However, oscillation of the period (8–10 yr) and amplitude observed (Fig. 1) is obtained when the a parameters are increased by about 2 (to −3.47 and −3.91), especially if herring recruitment is modelled with random normal environmental effects (W_t) added to Z_t.

A variety of other regression models were fitted to the recruitment time series, using various combinations and components of the prey and predator stock sizes as predictors along with environmental indices such as sea surface levels and temperatures. None of these models gave substantially better fits to the data, although they helped us identify one basic confounding of factors. Cod and herring stock sizes are inversely correlated (Fig. 2), so that it is impossible to distinguish whether low survivals from high herring egg depositions are due to competition–cannibalism within the herring stock (b parameter), or heavy predation later in life by cod (q parameter). To emphasize this point, Fig. 5 shows the fit to the herring time series of the model

$$(5)\quad R_{t+1} = E_t \exp[-6.135 - 0.1758P_t]$$

where P_t = age 2+ cod abundance (i.e. including juvenile cod as predators). This model assumes no density dependence at all in the herring recruitment dynamics ($b = 0$), and instead generates a "dome-shaped" relationship due to the apparent numerical response of the cod. Interestingly, a good fit to the cod recruitment series cannot be obtained by a similar model change; density independence plus herring abundance leads to a cod recruitment model that predicts peak recruitments out of phase with the estimated time series.

Comparing Fig. 3 and 4, it appears that the production of strong cod year classes may require a series of good recruitment years for herring, through some effect such as cumulative increase in cod fecundity or survival over several years of good food conditions. To test this possibility, we fitted the cod recruitment data to an extended version of equation (2.5) (see Table 2) with herring age 1 recruits the previous two years included as P_{t-1}, P_{t-2}, along with the current herring recruitment P_t. The resulting equation was

$$(6)\quad R_{t+1} = E_t \exp[-6.29 - 3.16 \times 10^{-4}E_t + 1.44 \times 10^{-5}P_t + 6.00 \times 10^{-5}P_{t-1} + 6.51 \times 10^{-5}P_{t-1}].$$

The predictions of this equation (Fig. 6) are a bit better than equation (2.4), but it is still unable to explain the sharpness of the 1961–62 peak in cod recruitment. Perhaps it is worth noting at this point that Fournier (1983) did not estimate the 1961–62 recruitment peak to be so large (compared with other years) as we have assumed in using VPA estimates.

Table 2 presents estimates of average total mortality rates in the first year of life due to density-dependent mortalities ($b\bar{E}$) and predation ($q\bar{P}$). For example, the estimate $q\bar{P} = 0.75$ for equation (2.3) implies that the baseline instantaneous mortality rate of 5.47 for the herring first year of life is increased by 0.75 when the cod stock is at its average level of $\bar{P} = 3.0$ million fish. Note that as shown in Fig. 3, equation (2.3) predicts the herring Z remarkably well, and ascribes a total range of variation of around 1.5 (from 6.5 to 8.0) in this rate to cod predation. This surprisingly high contribution to apparent mortality can be understood by examining the estimate of q (0.249) more closely. In equation (2.3), q is interpreted crudely as the probability of juvenile herring mortality per million cod present in the system, i.e. $q\bar{P} \approx$ (number of juvenile herring eaten)/number at risk to cod). According to this interpretation, we can estimate the annual herring consumption per million cod as q × (number at risk). If juvenile herring are mainly eaten in the winter months as they approach their first birthday, then the number at risk is best estimated by the age 1 recruitment R_t rather than the massively larger larval production E_{t-1}. Using the average age 1 herring abundance (3870 million) as the mean number at risk, we obtain the estimate (0.249) (3870) = 963 juvenile herring consumed per cod per year. This estimate is substantially higher than expected on the basis of stomach contents or growth energetics arguments (see above). Obvious explanations for the discrepancy include the following: (1) we may have underestimated cod abundace P_t using a conservative VPA procedure; (2) herring abundance may be overestimated by the Fournier procedure; and (3) we may in fact be estimating a total mortality rate that is spread across several years of the herring's life, rather than concentrated around the first birth-

TABLE 2. Stock–recruitment models for cod and herring, estimated by multiple regression from data in Table 1. R_t = age 1 recruits; E_t = effective egg deposition; P_t as defined. The $b\bar{E}$ and $q\bar{P}$ are measures of average total mortality rate attributable to density and interaction dependence, respectively.

Ricker models (equation (1))

(2.1) Herring: $R_{t+1} = E_t \exp\{-6.14 - 2.133 \times 10^{-7} E_t\}$ $\quad b\bar{E} = 1.31$

(2.2) Cod: $R_{t+1} = E_t \exp\{-5.49 - 3.949 \times 10^{-4} E_t\}$ $\quad b\bar{E} = 1.20$

Interaction models (equation (2))

(2.3) Herring: $R_{t+1} = E_t \exp\{-5.47 - 2.002 \times 10^{-7} E_t - 0.249 P_t\}$ $\quad b\bar{E} = 1.23$, $q\bar{P} = 0.75$

(2.4) Cod: $R_{t+1} = E_t \exp\{-5.91 - 4.072 \times 10^{-4} E_t + 1.475 \times 10^{-4} P_t\}$ (P_t = adult herring abundance) $\quad b\bar{E} = 1.23$, $q\bar{P} = 0.45$

(2.5) Cod: $R_{t+1} = E_t \exp\{-5.68 - 3.719 \times 10^{-4} E_t + 3.074 \times 10^{-5} P_t\}$ (P_t = age 1 herring abundance, year $t+1$) $\quad b\bar{E} = 1.13$, $q\bar{P} = 0.12$

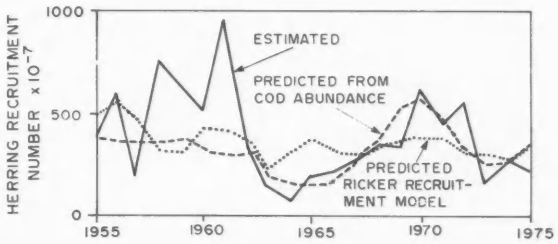

FIG. 3. Herring year class strength, estimated by Fournier method, compared with stock–recruitment predictions from Table 2.

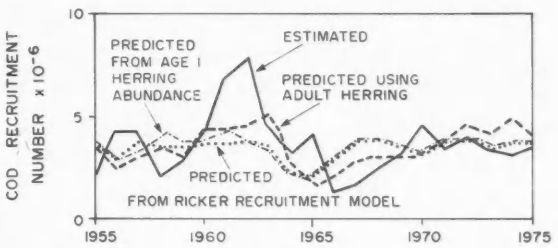

FIG. 4. Cod year class strength, estimated from VPA, compared with stock–recruitment regression predictions from Table 2.

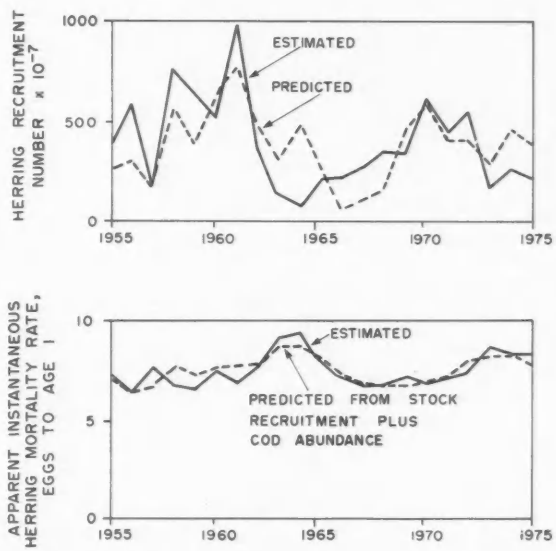

FIG. 5. Fit to the herring recruitment time series of a model assuming no density dependence in herring juvenile survival but predation by juvenile and adult cod. Predictions are from equation (5).

day. In view of these possibilities, the $q\bar{P}$ estimates in Table 2 are not unreasonable.

Discussion

Most previous research on Pacific cod and herring has sought explanations for recruitment variation in terms of abiotic environmental factors and overfishing during the peak herring reduction fishery of the early 1960s (Hourston 1980; Fournier 1983; Stocker et al. 1985). Recently, D. M. Ware and M. Stocker (ms in prep.) have questioned such explanations for herring on the west coast of Vancouver Island, and have suggested that predation, especially by Pacific hake (*Merluccius productus*), may be an important cause of recruitment variation. We examined sablefish predation as well in the Hecate Strait workshop, but concluded that it is unlikely to be a major factor in the Hecate Strait. By examining recruitment relationships statistically in terms of the log recruits per spawner Z_t, we have presumably accounted for basic variations in recruitment due to recruitment overfishing; equations (1) and (2) propose that recruitment is proportional to spawning stock when the stock is very low, with the proportionality constant determined by fecundity and the Ricker parameter "a".

Several lines of evidence support the possibility that predator–prey interactions have been a major determinant of recruitment variation in the Hecate Strait. First, there is a broad cline in herring recruitment variability along the British Columbia coast (Fig. 2), with recruitments being less variable and not apparently cyclic where cod are less abundant. Associated with this cline is an increase in the Ricker "a" parameter for herring stock–recruitment; Walters et al. (1982) estimated that the Georgia Strait herring have a Ricker "a" parameter about

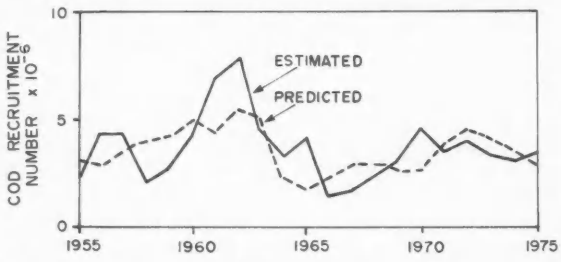

FIG. 6. Prediction of cod recruitment using Ricker stock–recruitment relation plus herring recruitments of past years (equation (6)).

0.2–1.0 larger (i.e. Z, 0.2–1.0 smaller) than the other stocks shown in Fig. 2. Second, better statistical fits to the recruitment time series are obtained by using predator and prey abundances as predictors than are obtained with any individual environmental indices identified to date. The simple recruitment equations that we have tested do not fully explain the recruitment variations, especially over the 1957–62 period, but there are indications (Fig. 6) that we may simply have failed to identify the correct timing and delay structure for when herring are eaten and how this consumption is translated into cod recruitment and survival. Finally, the estimates of herring consumption per cod based on recruitment regression analysis are not wildly divergent from expectations based on diet composition and energetics, although these estimates suggest that we have overestimated the impact at least of adult cod. Information on numbers and size of herring in cod stomachs will be available soon (D. Hay, pers. comm.). Such information will allow the development of much more precise expectations, and will give clues about the best regression model structures to use instead of equation (2).

Assuming that cod predation rates are an additive component of the herring natural mortality rate, there is still considerable ambiguity about what mechanisms drive the "cycle" evident for the Hecate Strait in Fig. 2. At least three alternative biotic explanations are partly consistent with the data. First, there may be a basic predator–prey instability in the classical sense, with increases in herring stimulating increases in cod which then drive the herring down which then results in a cod collapse. Our regression models equations (2.3) and (2.4) are capable of producing such cycles after some adjustment in parameter estimates. Second, the herring stock–recruitment relationship may be strongly dome shaped (due to competition, cannibalism) enough to cause herring abundance cycles even in the absence of cod predation; cod may just track these cycles without significantly reinforcing them. Such a model could not explain the geographic pattern in Fig. 2, since it would predict stronger cycling in the more productive Georgia Strait herring stock. Third, the cod may cycle due to a dome-shaped recruitment relationship, without being significantly affected by herring, and the herring may simply track the cod cycle. Equation (5) reflects this possibility, and it is supported by stomach contents data which indicate that the cod are not dependent on herring except perhaps in winter just prior to spawning.

Simulation trials of equations (2.3) and (2.4), but with randomly varying environmental effects on herring recruitment, indicate that occasional production of strong herring year classes can maintain or exaggerate an otherwise weak predator–prey cycle. Such an "environmental forcing" hypothesis is consistent with the regression results in Fig. 3 and 4, especially if the herring and cod have opposite survival responses to the environmental factor(s) involved. For example, high transport northward through the Strait during late winter may be unfavorable for larval cod survival, but favorable to larval herring survival by holding the larvae in more productive inshore waters (A. V. Tyler and S. J. Westrheim, unpubl. data). It is noteworthy that the relatively enclosed, inshore environment of the Georgia Strait provides good survival conditions for herring but apparently poor conditions for cod.

The relatively poor fit of the model to the 1961 herring year class is likely due to the influence of a physical oceanographic factor. Apparently some coast-wide phenomenon enhanced recruitment of a number of species in various locations: for example, Pacific halibut (*Hippoglossus stenolepis*) in the Gulf of Alaska (Deriso 1985), English sole (*Parophrys vetulus*) off Oregon (Hayman et al. 1980), and Pacific hake off southern California (Bailey 1981). Consequently, we would not expect the predation model to "predict" abundance this year.

The major herring reduction fishery off British Columbia collapsed in 1966–68, and this collapse has been attributed to overfishing causing weak year classes in 1963–65 (Hourston 1980). The predator–prey hypotheses outlined above suggest an alternative scenario for events leading to the collapse. According to these hypotheses, the trouble really began in the late 1950s, when either historical cod-herring "imbalance" or some environmental forcing factor led to the production of exceptionally strong herring year classes. The strong herring year classes led to very strong cod year classes in the early 1960s, and these cod caused very poor herring recruitment in the mid-1960s. Considering that similar herring declines occurred both before and after (late 1970s, early 1980s) the reduction fishery collapse, we must consider whether the fishery and its management have had much impact at all on changes in herring abundance. This argument is reminiscent of the Thompson–Burkenroad debate (Skud 1975) and other more recent examples (Skud 1983) of controversy about the relative importance of environmental factors (including predation) versus management in the declines and recoveries of stocks.

Fishing efforts and exploitation rates for cod have been relatively high in the 1970s and 1980s (Westrheim and Foucher 1985; Fournier 1983), and this appears to be associated with relatively high and stable recruitment rates. Our predator–prey models (Table 2) suggest two possible scenarios for the next decade. If the herring recruitment relationship is not dome shaped, then low recruitment rates will gradually increase as will the stock size, due to the present relative scarcity of cod. Alternatively, if the herring recruitment relationship is dome shaped, then there may be a resurgence of the herring stock followed by more violent, longer period oscillations (due to a higher Ricker "a" value for herring if cod are held down by fishing). Neither of these scenarios is particularly hopeful for herring management, and they suggest the need to search for cod–herring "co-management" strategies that may prevent the two fisheries from destabilizing each other's fishing opportunities. The search for such strategies is an exciting area for further research.

Conclusion

Much evidence points to the existence of a cod–herring interaction in the Hecate Strait, and if it is strong this interaction has important management implications. Obviously, biological studies are necessary now to establish the distribution,

behavior, and diet of both cod and herring at ages 0 and 1. This is the only likely time during which substantial cod–herring interactions could take place in Hecate Strait.

However, it remains possible that the appearance of "cycles" in abundances has resulted from a mere coincidence of factors in the short time series now available, or from environmental forcing that affects the species in opposite directions. The environmental forcing hypothesis cannot be tested merely by patiently gathering longer time series in conjunction with more detailed studies on recruitment biology. Both it and the predator–prey hypotheses predict continued, fairly regular fluctuations into the future if historical fishing patterns are maintained. A bold step now would be to seek an experimental fishing policy that would manipulate cod and herring stock sizes to levels where the various hypotheses make distinctive predictions. Without such a deliberate experiment, we may remain forever uncertain about the importance of the predator–prey interaction.

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Wind Stress and Cycles in Dungeness Crab (*Cancer magister*) Catch off California, Oregon, and Washington

David F. Johnson[1]

Bodega Marine Laboratory, P.O. Box 247, Bodega Bay, CA 94923, USA

Louis W. Botsford

Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616, USA

Richard D. Methot, Jr.

National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038, USA

and Thomas C. Wainwright

Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616, USA

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Dungeness crab (*Cancer magister*) catch records along the coasts of northern California, Oregon, and Washington covary in a cyclic pattern with a period of 9–10 yr. Both environmental forcing and density-dependent recruitment have been proposed as the mechanisms causing these cycles. Spring wind stress in a southward direction is correlated with crab catch along this coast at typical lags of 4 and 5 yr. This time lag corresponds to the time required for growth from the larval phase to the size caught in the fishery. Also, computed autocorrelations show that wind stress is itself cyclic. Since crab larvae appear to be transported offshore and northward during the early larval phase, the observed correlation may result from a dependence of subsequent successful settlement on wind-driven southward, onshore transport during the late larval phae in the spring. However, the exact mechanisms are not known. The computed correlations indicate that wind stress may contribute to the observed cycles.

Les prises de crabes dormeurs (*Cancer magister*) effectuées le long des côtes du nord de la Californie, de l'Orégon et de l'État de Washington présentent un même cycle dont la période est de 9 ou 10 ans. On a tenté d'expliquer ce phénomène par les mécanismes des contraintes environnementales et du recrutement dépendant de la densité. La contrainte due au vent de printemps qui souffle en direction sud présente une corrélation, typiquement décalée de 4 ou 5 ans, avec les prises de crabe effectuées le long de cette côte. Ce décalage correspond au temps nécessaire pour passer du stade larvaire à la taille commerciale. Des autocorrélations ont aussi permis de montrer que la contrainte due au vent était elle-même cyclique. Les jeunes larves de crabe étant transportées vers le large en direction nord, la corrélation observée pourrait elle-même être fonction de la réussite de l'établissement des larves âgées qui sont transportées par le vent en direction sud au printemps. Le détail de ces mécanismes demeure cependant obscur. Les corrélations obtenues indiquent que la contrainte due au vent pourrait jouer un rôle dans les cycles observés.

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Periodic fluctuations in the annual catch of the Dungeness crab (*Cancer magister*) have been under investigation for almost two decades (Pacific Marine Fisheries Commission 1965, p. 38). These cycles of period 9–10 yr are evident in the catch statistics of northern California, Oregon, and Washington (Fig. 1). The central California population collapsed to low levels near 1960 and is not investigated here (see Wild and Tasto 1983).

Three types of mechanisms have been proposed as potential causes of the observed cycles: (1) a predator–prey interaction, (2) density-dependent recruitment, and (3) an environmental factor. The first possibility has been discounted for both man (Botsford et al. 1983) and chinook salmon (*Oncorhynchus tshawytscha*) (Botsford et al. 1982) as the predator. The second type of mechanism is still under analytical and field investigation (Botsford and Wickham 1978; McKelvey et al. 1980; Botsford 1981, 1984; McKelvey and Hankin 1981; Botsford et al. 1983), and the hypothesis that a mechanism of this kind is causing the cycles has not been rejected.

[1]Current address: NOAA/MEAD, 3300 Whitehaven St. NW, Washington, DC 20235, USA.

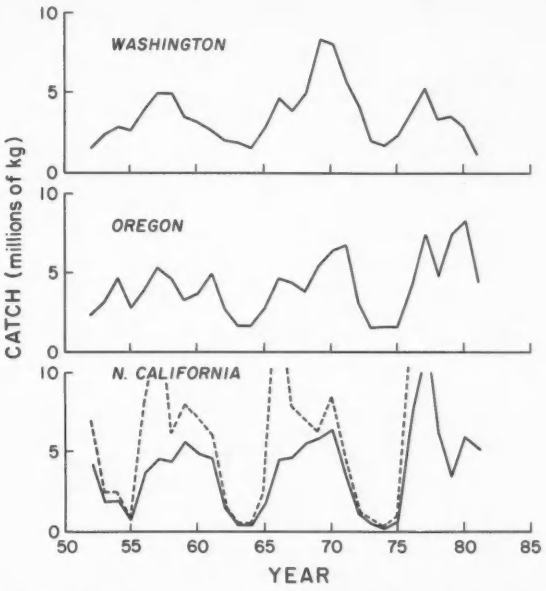

FIG. 1. Dungeness crab catch record for Washington, Oregon, and northern California. Broken line is an estimate of preseason abundance (Methot and Botsford 1982). The year given is the year during which most of the season occurs (i.e. the season from December 1975 to summer 1976 is identified as 1976).

The third potential mechanism was first proposed on the basis of observations that the cycles in annual crab landings are coastwide and apparently synchronous (Pacific Marine Fisheries Commission 1965, p. 38). The effects of temperature and salinity on the larval stages were evaluated in the laboratory, but local environmental extremes in these variables were deemed insufficient to cause large larval mortalities (Reed 1969). Upwelling, summed over the spring and summer, was found to be correlated with Dungeness crab catch, but the maximum correlation occurred for crab catch following upwelling by 0.5 and 1.5 yr (Peterson 1973). These lags required a mechanism by which upwelling influenced adults rather than the larval stages, as might be expected. Because upwelling itself was not cyclic, and the lag between upwelling and catch was less than 1 yr, Botsford and Wickham (1975) concluded that it was not driving the cycles in catch. Wild (1980) and Wild et al. (1983) noted that troughs in the northern California catch record were associated with peaks in the winter sea surface temperature record. Based on this observation and laboratory studies, they concluded that the troughs in the northern California cycles were caused by anomalously high bottom temperatures that adversely affected the survival and hatching success of crab eggs.

Although several environmental variables have been proposed and evaluated to varying degrees, none has satisfied the three basic requirements that (1) there is a significant correlation between the environmental variable and crab catch, (2) the environmental variable itself appears cyclic over the time period of interest, and (3) there is a plausible biological/physical mechanism that could cause the observed statistical relationship.

Based on a suggestion that the fishery was heavily influenced by the survival of the pelagic stages (Cleaver 1949), the Pacific Marine Fisheries Commission (1965) suggested that changes in local ocean-circulation patterns in some years might transport crab larvae away from preferred habitats, resulting in abnormally high mortality and subsequently poor commercial catches. Our purpose in the research presented here was to determine whether available data indicate that variations in currents and wind stress during the larval phase of the Dungeness crab influence subsequent commercial catch. We first describe the larval phase and potential oceanographic influences, and then test whether variations in wind and oceanographic variables that indicate the strength of currents are correlated with Dungeness crab catch and are themselves cyclic.

Larval Drift

Existing knowledge of phenology and distribution of the larval phase together with general coastal circulation patterns can be used to design specific tests of likely oceanographic influences on larval transport. Adult *C. magister* occur from the low tide line to depths of 230 m, but are most abundant near shore at depths less than 90 m (Morris et al. 1980). They range from the Alaskan Peninsula to southern California (Morris et al. 1980). Larvae hatch from January to early March off northern California and Oregon (Waldron 1958). The larvae spend 3–4 mo in the plankton while passing through five zoeal and one megalopal stage, and then settle and metamorphose to juvenile crabs. In central California the five zoeal stages are believed to take 80–90 d whereas the megalopal stage takes 25–30 d (Reilly 1983). The larval season extends from late December through June because of variability in hatching time. The megalopae are most abundant in May and June off Washington (Cleaver 1949) and April to June off northern California (Morris et al. 1980).

The general behavior of winds and currents during this period implies a potential for northward larval transport during the early larval period, and then southward transport during the late larval period. During the early winter months when hatching occurs, the northward flowing Davidson Current is usually well established inshore of the southward flowing California Current. The Davidson Current is approximately 90 km wide and is a result of local wind stress predominantly from the southwest (Burt and Wyatt 1964). Estimates of the surface velocity of the Davidson Current indicate a northward flow of approximately 8–20 km/d (Reid and Schwartzlose 1962; Wyatt et al. 1972). Highest densities of first-stage zoeae off Oregon occur between 5 and 15 km from shore where larvae would be transported northward by the Davidson Current (Lough 1976). During the early winter months, winds are toward the north, but shift to an onshore and then southerly direction in March or April. Near the time of this shift in wind direction the Davidson Current weakens on the surface and is replaced by a generalized southward flow. In some winters, severe winds from the northwest may effectively counter the northward flow of the Davidson Current at the surface for periods of a few days to a couple of weeks or may hasten the seasonal reversal of flow, but typically the seasonal shift to southward flow occurs by March or April (Burt and Wyatt 1964). Because the early zoeal stages may behave differently than the later megalopal stage, and winds and currents shift from a general northerward direction to a southward direction in early spring, we divided the larval phase into two periods, early (January, February, March) and late (April, May, June), and analyzed the effects of environment on each.

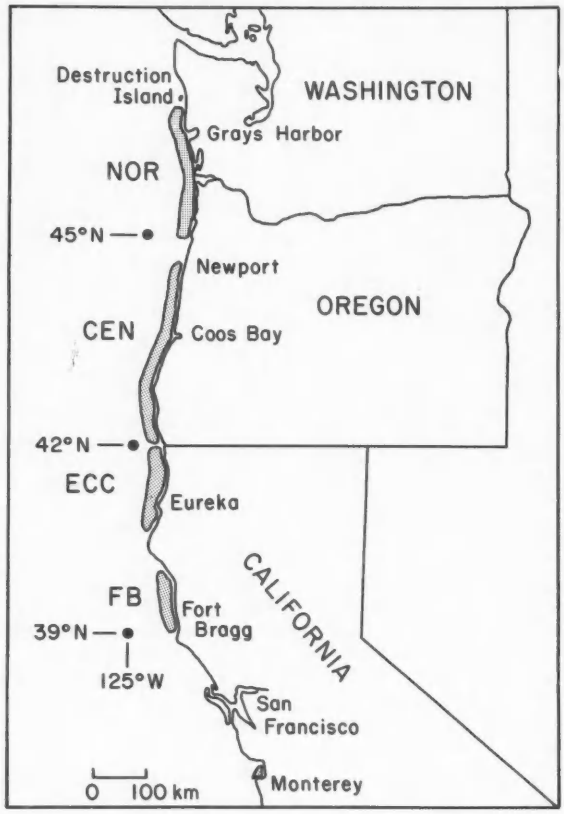

FIG. 2. Major Dungeness crab fishing areas (modified from Pacific Fisheries Management Council 1979) (stippled area). Wind locations used in the analyses (39°N × 125°W, 42°N × 125°W, and 45°N × 125°W).

Methods and Data

Since estimates of annual settlement rates for Dungeness crab young of the year are unavailable over a long time period, we have used commercial catch statistics to reflect year class size. Preseason abundance estimates for northern California (Methot and Botsford 1982) indicate that, with the exception of the initial high years of a cycle which have lower harvest rates and the initial low years of a cycle which have higher rates (see Botsford et al. 1983 for further explanation), catch is a high constant fraction of legal abundance. To test the importance (to the environmental forcing issues) of years that do not have the typical harvest rates, we have also examined the relationship between environmental variables and the preseason abundance estimates.

The catch data are reported by port of landing for fishing seasons from 1950–51 to 1980–81, except for Oregon where these records begin with the 1951–52 season (Pacific Marine Fisheries Commission 1983). Catch records by port of landing were pooled for each of four major fishing areas along the United States west coast (Pacific Fisheries Management Council 1979) (Fig. 2). These are referred to as Washington – northern Oregon (NOR), central and southern Oregon (CEN), Eureka – Crescent City (ECC), and Fort Bragg (FB). These fishing areas do not represent isolated stocks. Tagging studies indicate that crabs travel between the northern California (ECC) and southern Orgon (CEN) areas, and that along the Oregon and Washington coasts up to Destruction Island there are no barriers to movement (Cleaver 1949; Jow 1965; Waldron 1958; Snow and Wagner 1965; Demory 1971). However, there is no concerted direction of movement and most of the crabs tagged do not travel far. Previous analyses of Dungeness crab catch records have involved the total northern California catch, corresponding to the sum of the catch from ECC and FB fishing areas (e.g. Botsford and Wickham 1975). These fishing areas are treated separately in this analysis because they are separated geographically and there is no evidence of benthic exchange between them. However, they are not of equal importance here, since mean catch at Fort Bragg is only 8.7% of ECC catch.

Ten-day averages of the wind data in terms of wind speed, wind stress, and the cube of the wind speed were supplied by Andrew Bakun (Pacific Environmental Group NMFS/NOAA, Monterey, CA) for points along the west coast of the United States for the years 1946–78. These wind speeds and directions were computed from barometric pressure measurements using a method that is similar, but not identical, to the method used in computing winds for Bakun's (1973, 1975) upwelling index (Caton et al. 1978). Wind data from locations closest to the four major commercial crabbing areas were selected: 39°N × 125°W, 42°N × 125°W, and 45°N × 125°W. The shift in wind direction described above can be seen in the averages for each month (over the years 1946–78) (Fig. 3).

Time series of three oceanographic variables were used as possible indicators of currents: sea surface temperature, sea level height, and Bakun's upwelling index. Sea surface temperature and sea level height are associated with changes in alongshore flow (Enfield and Allen 1980; Chelton et al. 1982; McLain and Thomas 1983), and upwelling is associated with flow in the onshore–offshore direction (e.g. Bakun 1973, 1975). Sea surface temperatures (supplied by D. McLain, Pacific Environmental Group, NMFS/NOAA, Monterey, CA 93940) consist of measurements by ships of opportunity. As supplied, these values are averaged over the 5° latitude by longitude "Marsden squares" adjacent to the coast from 35°N to 40°N, 40°N to 45°N, and 45°N to 50°N. Sea level height was recorded at coastal tide gauge stations at 38°N, 42°N, and 48°N (also supplied by D. McLain). The upwelling time series were estimated from computed onshore–offshore components of Ekman transport that would result from winds computed from barometric pressure measurements (Bakun 1973, 1975). The latitudes used were 39°N, 42°N, and 45°N.

Although we used catch data to represent annual recruitment, recent evaluation of Dungeness crab growth rates indicates the commercial crab catch does not reflect recruitment of a single year class but rather is composed of at least two year classes. About 50% of a year class enters the fishery (i.e. becomes larger than the minimum legal size, 159 mm carapace width) at age 4 with most of the remaining half entering the fishery at age 5, although small numbers enter the fishery at ages 3 and 6 yr (Botsford 1984). Also, the harvest rates estimated by Methot and Botsford (1982) imply substantial carryover in northern California in high-abundance years. To account for this, some correlations were also computed for 2-yr running means of the environmental variable with crab catch.

The covariation of each of the time series of wind and

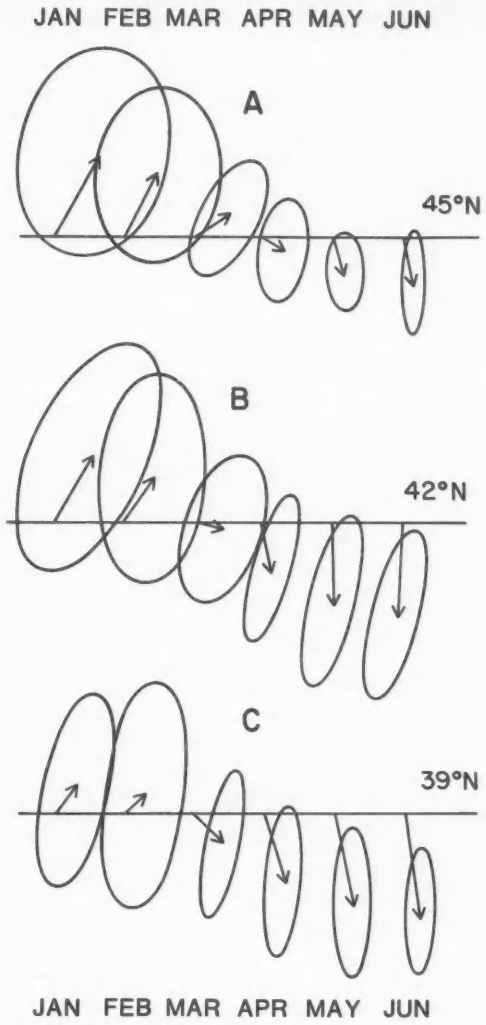

FIG. 3. Mean wind stress for the winter and spring months at locations used in the analysis (39°N × 125°W, 42°N × 125°W, and 45°N × 125°W). Ellipses indicate the computed standard deviations.

oceanographic data with the appropriate catch series of the Dungeness crab was evaluated by computing the cross-correlations between them for both the early larval period (January–March) and the late larval period (April–June). Autocorrelations of time series of environmental variables with significant cross-correlation and time series of crab catch were also calculated to evaluate the periodic nature of each series. Linear trends were removed from each series before computing correlations.

Because wind stress is a vector quantity and little is known of the mechanisms by which it might affect settlement, it is useful to determine the direction of the best statistical relationship between wind stress and later crab catch. There are several different ways of defining the best statistical relationship, and each of them leads to an analytical expression for the best direction (Mooers 1973; Garrett and Toulany 1982; Enfield and Allen 1983). The definition used here is the direction of maximum cross-correlation. However, since we are interested in the strength of the maximum (relative to the adjacent directions) and we are concerned with several different lags and different locations, we present computed correlations every 22.5° for each lag and location, rather than just the direction of maximum correlation.

Correlations computed here are defined for two series x_n and y_n as

$$(1)\quad R_{xy}(k) = \frac{\sum_{n=1}^{n-|k|} (x_n - m_x)(y_n - m_y)}{(N - |k|)\, s_x s_y}$$

where k = lag, N = number of data points in series, s_x and s_y = standard deviations computed from all N points, and m_x and m_y = means computed from all N points. For autocorrelations, x_n and y_n would be the same series. This expression differs from one often used in time series (e.g. in Box and Jenkins 1976). In Box and Jenkins' expression the divisor contains N rather than $N - |k|$. The correlation is expressed in that way to maintain the property of semidefiniteness, even though it yields a biased result. We have used $N - |k|$ because (1) we do not require positive semidefiniteness, since we will not be transforming the correlation, and (2) it yields an unbiased estimate that is similar to the standard univariate, static definition of correlation coefficient (cf Snedecor and Cochran 1980).

In addition to the usual problems involved in interpreting single correlation coefficients, interpretation of autocorrelation and cross-correlation functions is hampered by the fact that the samples from which they are computed (i.e. adjacent data points) are not necessarily independent. Thus, strictly speaking, the usual expressions for variance do not apply. There are several ways of accounting for intraseries correlation in computing the variance of computed correlations. Box and Jenkins (1976, p. 34 and 376) and others (e.g. Fuller 1976) recommended use of Bartlett's (1946, 1966) formula and various large lag approximations to it. Sutcliffe et al. (1976) used Bayley and Hammersley's (1946) expression for the variance of autocorrelations in evaluating the cross-correlation between physical variables. Both of these expressions, however, assume a long data series (i.e. a large sample size). Because this assumption does not hold in this case, an expression similar to Bartlett's (1966) expression that does not depend on the assumption of large N (L. W. Botsford and T. C. Wainwright, unpubl.) was used here:

$$\begin{aligned}\operatorname{var}[R_{xy}(k)] = \frac{1}{N - |k|} \sum_{b=-(N-k)+1}^{n=N-k-1} \left[1 - \frac{|n| + k}{N}\right] \\ \times \Big[R_{xx}(n)R_{yy}(n) + R_{xy}(n+k)R_{yx}(n-k) \\ + R_{xy}^2(k)\{R_{xy}^2(n) + \tfrac{1}{2}R_{xx}^2(n) + \tfrac{1}{2}R_{yy}^2(n)\} \\ - 2R_{xy}(k)\{R_{xx}(n)R_{xy}(n+k) \\ + R_{xy}(-n)R_{yy}(n+k)\}\Big].\end{aligned}$$

This expression is used for both auto- and cross-correlation functions. One of the obvious problems with expression (2) (and with the aforementioned expressions) is that the variance of the correlation that we are attempting to estimate (or detect) depends on values of the correlations at that lag and all other lags. To compute this variance we therefore use computed correlations $R_{xy}(m)$ as estimates of the true values.

TABLE 1. Correlations (R) at lag zero between catch in the various fishing areas. All values are significant ($P < 0.05$) by both the correlated and the uncorrelated series tests.

	NOR	CEN	ECC	FB
NOR	1.000	—	—	—
CEN	0.436	1.000	—	—
ECC	0.524	0.677	1.000	—
FB	0.476	0.506	0.633	1.000

Correlations computed herein are compared with 1.96 $(\text{var}[R_{xy}(k)])^{0.5}$ which would correspond to a 95% confidence limit if the distribution of computed correlations were Gaussian. This is referred to here as the small sample test. Because use of computed correlations introduces some variability into the confidence limits themselves, and to provide the means to evaluate the magnitude of correlation coefficients in more usu¬l terms, we also compare computed correlations with 1.96 $(1/(N - |k|))^{0.5}$. This corresponds to testing whether a computed value is different from zero assuming that autocorrelations at all lags (except lag zero) are zero, and hence is referred to here as the uncorrelated series test. This standard error is approximately the same as the standard tables for correlation coefficients (cf. Snedecor and Cochran 1980).

Results

Estimates of cross-correlation between catch records at the locations identified in Fig. 2 show a moderately high degree of coherence among the fishing areas (Table 1). Values of these correlations at lag zero were greater than values at other lags in all cases.

The most promising statistical relationship observed was between southward winds during the late larval period (April–June) and crab catch 3.5 and 4.5 yr later. We first determined the wind direction of maximum correlation. The distribution of correlations over wind direction, location, and lag (Table 2) revealed a maximum correlation in a southerly direction and typically at lags of 3.5 and 4.5 yr (somewhat earlier in ECC and FB, and later in CEN). From estimated growth rates (Botsford 1984), these lags correspond to the time from the larval stage to entry into the fishery. There is not a sharp maximum in the southerly direction, but rather correlations are significant over a range of southerly directions. On the basis of this information, we used southward winds at each location in subsequent analysis.

Correlations between southward spring wind stress (April–June) among the three locations used in this analysis indicate a high degree of coherence over the range of the four crabbing areas (39°N vs. 42°N is 0.940, 42°M vs. 45°N is 0.781, and 39°N vs. 45°N is 0.688). Thus, winds over this range exhibit a coherent coastwide influence as would be required for an environmental variable to be driving the coherent cycles of Dungeness crab catch. This coherence also obviates the need to closely match the likely location of the crab larvae with the nearest site of wind stress estimates.

To account for the fact that crab catch is composed primarily of two year classes, we computed the cross-correlation between a 2-yr running mean of southward wind during the late larval period crab catch at each location (Table 3). These correlations are generally greater than the former correlations. The number of degrees of freedom is reduced because of the intraseries correlation introduced by the running average, but this effect is theoretically accounted for by the small series test.

For this wind to be driving the cycles in crab catch, it should also appear cyclic over the time period for which data are available. The periodicity in the crab catch and the 2-yr running mean of southerly wind can be compared based on plots of the autocorrelation of each as a function of lag (Fig. 4 and 5). Negative peaks at lags of 4 and 5 yr followed by positive peaks at lags of 9 and 10 yr indicate a cyclic process. From Fig. 4 and 5, the wind series for each location appears to be as cyclic as the catch series.

Estimates of preseason abundance of legal Dungeness crabs in northern California provide another estimate of year class size that is free of the effect of variations in harvest rate. Estimates of cross-correlation between this time series and both spring wind stress at 42°N and the 2-yr running mean of spring wind stress at 42°N are given in Table 4. Two approaches are taken to accounting for the three years (1957, 1966, 1977) for which the preseason abundance was high but could not be estimated: (1) the years are treated as missing data and (2) a value of 10 Mkg is substituted for these years. The correlations that result from the former approach show a pattern that is similar to ECC in Tables 2 and 3, but correlations that result from the second approach show a pattern that is shifted to lower lags (Table 4). The 2-yr running mean again leads to stronger correlations.

Significant correlations between crab catch and oceanographic variables that are related to coastal flows would also reflect effects of the physical environment on larval transport. Computed correlations between crab catch and oceanographic variables (sea level height, sea surface temperature, and Bakun's (1973, 1975) upwelling index for the late larval period (April–June)) show occasional significant values, but exhibited no consistent pattern other than a significant correlation between upwelling and NOR catch at lags of 2, 3, and 4 yr. Computed correlations between crab catch and averages of sea level height, sea surface temperature, upwelling index, and north–south wind stress for the early larval period (January–March) also showed no consistent pattern.

Discussion

The correlations reported here between southward wind stress during the late larval period and later catch are significant at lags that are appropriate for an influence of wind on the larval phase. These correlations are significant by both tests used, and other similar tests (e.g. Bartlett 1966; Box and Jenkins 1976; Fuller 1976) would probably lead to similar results. The general usefulness of the small sample test used here is currently being further evaluated (L. W. Botsford and T. C. Wainwright, unpubl.).

Two aspects of the computed correlations are somewhat disconcerting. Similar correlations computed using the winds that form the basis of Bakun's upwelling index (Bakun 1973, 1975) show generally 1-yr lower lags and are not significant for CEN. These two wind estimates are computed differently and there has not been enough verification of them to determine which most closely represents the true winds. The second aspect is the low lag (2 yr) of significant correlations between southward wind during the late larval stages, and the preseason abundance estimates. This would indicate that the wind is not causing the high abundance years during the early part of each cycle. (Abundance during these years could not be estimated using the Leslie depletion method, but initial CPUE was high

TABLE 2. Cross-correlation between wind stress (April–June) in each of eight directions and crab catch at each location and lag. An asterisk indicates significance at the 0.05 level (uncorrelated series test).

		Direction (degrees)							
	Lag	90.0	112.5	135.0	157.5	180.5	202.5	225.0	247.5
NOR × Wind 45°N	3	−0.168	0.038	0.161	0.220	0.254	0.277	0.291	0.278
	4	−0.072	0.315	0.479*	0.532*	0.547*	0.540*	0.503*	0.389*
	5	0.071	0.425*	0.538*	0.555*	0.540*	0.506*	0.437*	0.281
	6	0.125	0.267	0.286	0.270	0.244	0.211	0.158	0.060
CEN × wind 42°N	3	−0.326	−0.105	0.121	0.219	0.270	0.304	0.331	0.351
	4	−0.443	−0.061	0.270	0.399*	0.460*	0.497*	0.522*	0.527*
	5	−0.159	0.293	0.507*	0.539*	0.531*	0.508*	0.468*	0.384*
	6	0.156	0.624*	0.690*	0.616*	0.537*	0.455*	0.353	0.186
ECC × wind 42°N	3	−0.073	0.297	0.444*	0.451*	0.431*	0.402*	0.359	0.276
	4	−0.253	0.212	0.475*	0.537*	0.549*	0.542*	0.517*	0.453*
	5	−0.027	0.303	0.414*	0.407*	0.382*	0.349	0.303	0.220
	6	0.350	0.456*	0.318	0.196	0.190	0.034	−0.049	−0.165
FB × wind 39°N	3	−0.208	0.101	0.239	0.304	0.344	0.376*	0.402*	0.399*
	4	0.005	0.288	0.371*	0.396*	0.402*	0.398*	0.377*	0.291
	5	0.397	0.343	0.239	0.165	0.102	0.036	−0.053	−0.206
	6	0.358	0.304	0.208	0.141	0.085	0.025	−0.055	0.191

TABLE 3. Cross-correlations between wind stress in a southerly direction and crab catch along with the cross-correlation between a 2-yr running mean of wind stress in a southerly direction and crab catch. (The lag in parentheses is the second year of the running mean.) An asterisk indicates significance at the 0.05 level by the uncorrelated series test and a dagger indicates significance at the 0.05 level by the small sample test.

	Lag	Wind stress	2-yr running mean of wind stress
NOR × wind 45°N	3 (and 4)	0.254†	0.248†
	4 (and 5)	0.547*	0.495*†
	5 (and 6)	0.540*†	0.672*†
	6 (and 7)	0.244	0.485*
CEN × wind 42°N	3 (and 4)	0.270†	0.253
	4 (and 5)	0.460*†	0.441*†
	5 (and 6)	0.531*†	0.586*†
	6 (and 7)	0.537*†	0.632*†
ECC × wind 42°N	3 (and 4)	0.431*†	0.482*†
	4 (and 5)	0.549*†	0.605*†
	5 (and 6)	0.382*	0.555*
	6 (and 7)	0.109	0.294
FB × wind 39°N	3 (and 4)	0.344*†	0.121
	4 (and 5)	0.402*†	0.516*
	5 (and 6)	0.102	0.351*†
	6 (and 7)	0.085	0.127

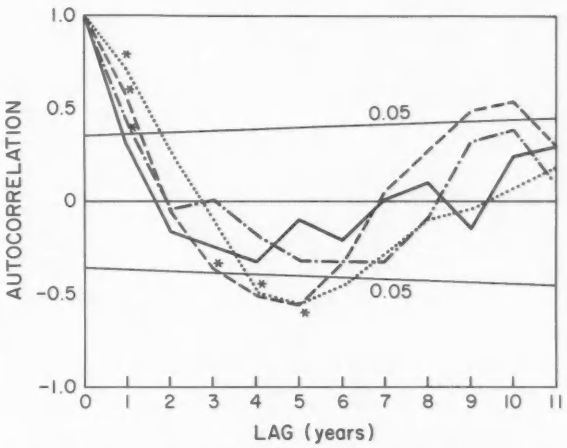

FIG. 4. Autocorrelation of crab catch at Fort Bragg (—), ECC (---), CEN (---) and NOR (···). The lines marked 0.05 indicate 0.05 significance levels by the uncorrelated series test. Asterisks indicate points that are significant at the 0.05 level by the small sample test.

(Methot and Botsford 1982).)

Complete definition of a mechanism by which southward winds could affect successful settlement will require more biological and physical oceanographic information than is currently available. Physical oceanography of the California Current system is extremely complex and not well understood, especially near shore (see Hickey 1979; Chelton 1984 for further information). The distribution of the larvae is also not well known. In the vertical direction, the early megalopal stage is typically associated with the surface more than the early (zoeal) stages (Reilly 1983; D. F. Johnson, R. D. Methot, Jr., and L. W. Botsford, unpubl. data). There is evidence for megalopae being in the neuston at night and diel vertical migration of megalopae (Booth et al. 1985; J. Shenker and L. W. Botsford, unpubl. data). Megalopae also cling to the pleustonic hydroid *Velella velella* (Wickham 1979; Reilly 1983; J. Shenker, unpubl.). In the cross-shelf direction, Reilly (1983), sampling over several years, found zoeal stages off San Francisco progressively further offshore, and then megalopae closer inshore. Lough (1976) found early zoeal stages inshore, no intermediate stages, and then megalopae inshore in one year, and only the early zoeal stages in a second year.

Larvae at the surface would be directly influenced by wind. Classical Ekman transport (Ekman 1905) would have them moving 45° to the right of downwind. However, when one considers that (1) transient wind effects are probably more important than steady-state effects (because of the high frequency content of wind variability), (2) a more realistic, vari-

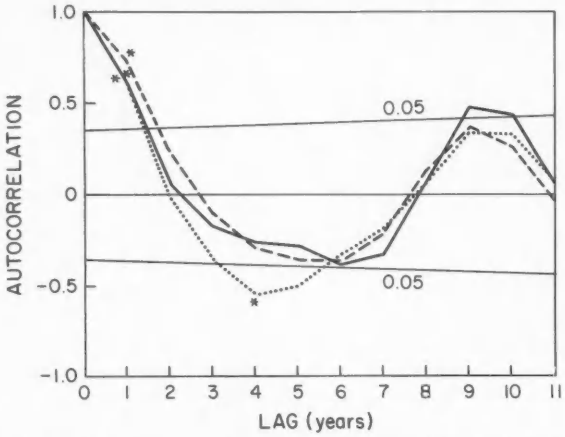

FIG. 5. Autocorrelation of southward wind stress at 39° (—), 42° (---) and 45° (···). The lines marked 0.05 indicate 0.05 significance levels by the uncorrelated series test. Asterisks indicate points that are significant at the 0.05 level by the small sample test.

able vertical eddy velocity leads to a lower angle (Madsen 1977), and (3) *V. velella* are transported 45° to 60° to the *left* of downwind on this coast (Ricketts et al. 1968), the implied direction of transport is closer to the actual wind direction.

The correlations reported here are consistent with a scenario in which zoeal stages are transported northward by the Davidson Current and successful return is enhanced by the influence of southward winds on the megalopae during the late larval period. The speed of the Davidson Current (9 km/d) implies that potential transport is considerable (800 km in the 3-mo period). Successful settlement may also depend on onshore transport. Classical Ekman theory would have the Ekman layer moving offshore with southward winds. However, (1) the megalopae may not be in the Ekman layer (i.e. they may be below it during the day, moving onshore) and (2) recent measurements show a much more erratic, event-oriented behavior than a constant offshore flow. This transport scenario is only one of several possible mechanisms. For example, the actual effect of the southward wind may be increased productivity rather than favorable transport. Better definition of the mechanism of wind influence will require direct sampling.

The results obtained here are consistent with results of similar studies of the central California population. Winnor (1966) found significant correlations at a lag of 4 yr between central California catch and three environmental variables averaged over January–April: local shore temperature (negative correlation), sea level height (negative correlation), and southward alongshore geostrophic winds (positive correlation). Correlation at the same lag between catch and onshore geostrophic winds was not significant. These correlations are consistent with southward transport being beneficial to crab larval settlement and, conversely, northward transport being deleterious.

In a recent study of the possible causes of the collapse of the central California fishery, the California Department of Fish and Game concluded that the oceanographic changes in the late 1950s (i.e. warmer temperatures, higher sea levels, stronger Davidson Current) may have precipitated the decline. The mechanisms proposed are (1) a deleterious effect of warmer water on egg survival and hatching success and (2) enhanced northward drift during the larval period because of a stronger Davidson Current.

TABLE 4. Cross-correlation between preseason abundance estimates (Methot and Botsford 1982) with the initial high years (1) treated as missing data and (2) assumed to be 10 Mkg and both southward wind stress at 42°N and a 2-yr running mean of southward wind stress at 42°N. (The lag in parentheses is the second year of the running mean.) An asterisk indicates significance at the 0.05 level by the uncorrelated series test.

	High years omitted		High years, 10 Mkg	
Lag	Wind stress	Running mean of wind stress	Wind stress	Running mean of wind stress
2 (and 3)	0.202	0.180	0.391*	0.348
3 (and 4)	0.474*	0.400*	0.396*	0.466*
4 (and 5)	0.339	0.481*	0.366	0.451*
5 (and 6)	0.266	0.358	0.240	0.358
6 (and 7)	0.191	0.276	0.149	0.235

With regard to northern California, Wild (1980) and Wild et al. (1983) noted the association between peaks in winter temperatures and troughs in crab catch 4 yr later. Although the purported mechanism was a deleterious effect of warmer water on egg production, the observed correspondence is consistent with the results obtained here. Higher sea surface temperatures are generally associated with a stronger Davidson Current and a weaker California Current. Thus, the negative association with temperature may reflect greater northward transport.

The statistical results reported here are consistent enough to allow the conclusion that they are probably not due to random chance; however, they do not constitute a proof of the proposed mechanisms. Rather, they present another hypothesis to explain the cyclic fluctuations in Dungeness crab catch, of equal status to the several other hypotheses (i.e. not yet disproven). This potential mechanism appears to be worthy of further investigation through direct field measurement and sampling.

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Evaluation of Factors Related to the Unusually Low Chlorophyll Levels in Prairie Saline Lakes

C. E. Campbell and E. E. Prepas

Department of Zoology, University of Alberta, Edmonton, Alta. T6G 2E9

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Prairie saline lakes in Canada have remarkably low chlorophyll *a* (Chl *a*) levels relative to total phosphorus (TP) and total nitrogen (TN) levels. To evaluate factors related to low Chl *a* levels, three Alberta saline lakes (total dissolved solids $> 5\ g \cdot L^{-1}$) were studied in 1983 and 1984. Mean summer phytoplankton Chl *a* ranged from 3 to 10 $\mu g \cdot L^{-1}$, mean summer periphyton Chl *a* was less than 70 $mg \cdot m^{-2}$, while mean summer TP and TN ranged from 2 to 13 and from 4 to 11 $mg \cdot L^{-1}$, respectively. Chl *a* and phytoplankton primary production were extremely low relative to predictions from measured TP and TN levels and empirical models for freshwaters. Bioassays indicated that inorganic phosphorus was not limiting, whereas inorganic nitrogen was limiting algal growth. Bacterial densities and zooplankton dry weight were high ($>10^7$ cells $\cdot mL^{-1}$ and $>1.0\ mg \cdot L^{-1}$, respectively) relative to predictions from Chl *a* and empirical models for freshwaters. Phytoplankton biomass was insufficient to maintain the zooplankton populations; bacteria and detritus were likely a major food source for zooplankton. This study suggests that freshwater models are not applicable to prairie saline lakes.

Dans les lacs salés des prairies au Canada, les concentrations de chlorophylle (Chl *a*) sont remarquablement faibles par rapport à celles de phosphore total (PT) et d'azote total (NT). Pour évaluer les facteurs qui sont liés aux faibles concentrations de Chl *a*, on a étudié en 1983 et 1984 trois lacs salés de l'Alberta (matières totales dissoutes $> 5\ g \cdot L^{-1}$). La concentration moyenne de Chl *a* du phytoplancton pendant l'été s'est située entre 3 et 10 $\mu g \cdot L^{-1}$, celle du périphyton a été inférieure à 70 $mg \cdot m^{-2}$, tandis que la concentration moyenne de PT et de NT pendant l'été a varié de 2 à 13 et de 4 à 11 $mg \cdot L^{-1}$ respectivement. La Chl *a* et la production primaire phytoplanctonique ont été extrêmement faibles si on les compare aux prévisions faites à partir des concentrations mesurées de PT et de NT et des modèles empiriques établis pour les eaux douces. Des tests biologiques ont montré que le phosphore inorganique n'était pas un facteur limitant, mais que l'azote inorganique limitait la croissance des algues. Les densités bactériennes et le poids sec de zooplancton étaient élevés ($>10^7$ cellules $\cdot mL^{-1}$ et $>1{,}0\ mg \cdot L^{-1}$ respectivement) par rapport aux prévisions faites à partir de la Chl *a* et des modèles empiriques établis pour les eaux douces. La biomasse de phytoplancton était insuffisante pour soutenir des populations de zooplancton; les bactéries et les détritus constituaient probablement une source importante de nourriture pour les organismes zooplanctoniques. Cette étude porte à croire que les modèles établis pour les eaux douces ne sont pas applicables aux lacs salés des prairies.

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While inland saline lakes (total dissolved solids (TDS) $>1000\ mg \cdot L^{-1}$) in many areas of the world often have high phytoplankton chlorophyll *a* (Chl *a*) levels (Hammer 1981), such high Chl *a* levels are uncommon in prairie saline lakes in western Canada. Saline lakes in central Alberta (Bierhuizen and Prepas 1985) often exhibit unusually low Chl *a* levels ($<10\ \mu g \cdot L^{-1}$) relative to extraordinarily high total phosphorus (TP) and total nitrogen (TN) levels ($>2000\ \mu g \cdot L^{-1}$). In the 18 Alberta saline lakes studied by Bierhuizen and Prepas, Chl *a* decreased significantly as salinity increased. Low Chl *a* levels have been reported for other saline lakes in western Canada such as in Manitoba (Barica 1978), Saskatchewan (Haynes and Hammer 1978), and in the dry interior of British Columbia (Topping 1975), although the relationship between Chl *a* and salinity levels was not quantified. Low Chl *a* levels thus appear to be a distinct characteristic of Canadian prairie saline lakes.

Several hypotheses could explain the low Chl *a* levels in the saline lakes on the Canadian prairies:

(1) Periphyton rather than phytoplankton is the dominant primary producer in these generally shallow saline systems, as Wetzel (1964) found in saline Borax Lake, California.

(2) Phytoplankton Chl *a* is not a good estimate of productivity in saline lakes due to unusually rapid algal turnover rates.

(3) Biologically available phosphorus, nitrogen, and iron levels are sufficiently low to limit algal growth dramatically, as reported in some saline lake studies (phosphorus limitation by Melack et al. (1982) and Kalff (1983), inorganic nitrogen limitation by Stephens and Gillespie (1976), iron and inorganic nitrogen limitation by Shubert (1978), phosphorus and inorganic nitrogen limitation by Moss (1969)).

(4) Extremely high densities of pelagic bacteria, similar to those reported for saline lakes with high organic content in East Africa (Kilham 1981), are diverting nutrients from the phytoplankton.

(5) High zooplankton populations are cropping the phytoplankton Chl *a* at unusually high rates, as Anderson (1958) suggested for saline Soap Lake, Washington.

To test these five hypotheses, three saline lakes in central Alberta (Fluevog, Peninsula and Oliva lakes; TDS $> 5000\ mg \cdot L^{-1}$) were studied from April 1983 to September 1984. Periphyton Chl *a* was measured to determine its relative impor-

TABLE 1. Location and morphometry of the three saline study lakes.

Lake	Lat.	Long.	Max. depth (m)	Mean depth (m)	Surface area (ha)
Fluevog	52°50′N,	111°19′W	2.1	1.4	32
Peninsula	52°52′N,	111°29′W	3.1	2.1	138
Oliva	53°05′N,	111°36′W	1.7	1.3	52

tance to total algal biomass. Phytoplankton Chl *a* and primary productivity were monitored to evaluate whether phytoplankton Chl *a* was a good estimate of primary production and to determine the relationship of these parameters to measured TP and TN levels. Phosphorus limitation was tested by ^{32}P-PO_4 uptake experiments on freshly collected lake water and by the addition of KH_2PO_4 to laboratory bioassays. Nitrogen, iron, and general nutrient limitation were tested by additions of NH_4Cl and KNO_3, iron chelate EDTA, and soil extract solution, respectively, to lake algal assemblages. To estimate bacterial abundance and the relative contribution of bacteria to secondary zooplankton production, pelagic bacteria populations were enumerated. To evaluate the impact of zooplankton grazing, zooplankton dry weight and population numbers were monitored and compared with phytoplankton biomass, and zooplankton grazing pressure was estimated. The data collected on the three saline lakes were then compared with empirical models developed for freshwater lakes.

Methods and Materials

Description of Study Lakes

The three saline lakes, Fluevog, Peninsula, and Oliva, are located in aspen prairie-parkland 150 km east of Edmonton, Alberta, and are surrounded by a mixture of ranch land and cultivated fields (primarily canola and flax). Annual rainfall in the region averages 300 mm, while annual lake evapotranspiration averages 600 mm (Fisheries and Environment Canada 1978). Average summer wind speeds are 13 $km \cdot h^{-1}$ (Environment Canada 1984). All of the lakes were shallow (mean depths 1.3−2.1 m) with small surface areas (<140 ha) (Table 1) and simple bowl-shaped basins. There were no permanent surface inflows or outflows from the lakes. Average summer turbidity was less than 15 JTU in Fluevog and Peninsula lakes and less than 2 JTU in Oliva Lake. The average summer Secchi depths (SD) in both Fluevog and Peninsula lakes were between 0.6 and 0.8 m, while in Oliva Lake, the disc was always visible on the lake bottom at 1.7 m. The three lakes are thus distinct from the highly turbid saline system in central Alberta studied by Daborn (1975).

Average summer conductivities ranged from 9400 and 13 400 $\mu S \cdot cm^{-1}$ in Fluevog and Peninsula lakes, respectively, where Na^+ and SO_4^{2-} were the dominant ions, to 55 000 $\mu S \cdot cm^{-1}$ in Oliva Lake where Na^+, SO_4^{2-}, and CO_3^{2-} were the dominant ions. (Details of ionic composition and TDS levels are in Bierhuizen and Prepas (1985); TDS in Oliva Lake was overestimated due to water retention and crystallization in the highly saline samples (American Public Health Association 1981).) Mean summer iron concentrations were 2.1, 1.5, and 0.6 $mg \cdot L^{-1}$ in Fluevog, Peninsula, and Oliva lakes, respectively (Bierhuizen and Prepas 1985). Both Fluevog and Peninsula lakes were isothermal over the year. Only Oliva Lake exhibited inverse summer stratification based on vertical profiles of conductivity and temperature. The lakes were never anoxic from March to September; DO levels were always >3 $mg \cdot L^{-1}$. Average summer pH was 9.2, 9.2, and 9.9, and alkalinity (milligrams HCO_3-CO_3 per litre) was 2160, 2600, and 22 660 in Fluevog, Peninsula, and Oliva Lake, respectively. Thus all three lakes can be characterized as alkaline, saline systems.

Species of plants and animals found in the study lakes were similar to those reported for other saline lakes in western Canada (Hammer et al. 1975; Hammer et al. 1983; R. S. Anderson, Alberta Environment, pers. comm.) and species diversity was low as is typical of highly saline environments (Williams 1972). The dominant phytoplankton species were *Microcystis aeroginosa* in Fluevog Lake, *M. aeroginosa* and *Lyngbya birgei* in Peninsula Lake, and a *Cryptomonas* sp. plus small (<30 μm long) diatoms such as *Fragilaria* and *Navicula* in Oliva Lake. Unidentifiable debris in the settling chambers made phytoplankton identification difficult. The major periphyton species were *Rhizoclonium hieroglyphicum* in Fluevog and Peninsula lakes and an unidentified filamentous green alga (*Pithophora* sp.?) in Oliva Lake. Macrophytes were scarce with only some *Ruppia* and *Carex* sp. present. There were only three species of zooplankton in each lake: *Diaptomus nevadensis*, *Diaptomus sicilis*, and *Daphnia similis* in Fluevog and Peninsula lakes and *Artemia salina*, *Brachionus plicatilis*, and a *Hexarthra* sp. in Oliva Lake. Ephydridae larvae were abundant during the summer in Oliva Lake. *Hyallela azteca* were common in Fluevog and Peninsula lakes. The lakes were fishless.

Field Collection

The three study lakes were chosen on the basis of their wide range of salinities, phytoplankton Chl *a* levels (Bierhuizen and Prepas 1985), and accessibility. Biweekly visits were made to each lake from April to September 1983 and 1984, and monthly visits were made over the winter. On each visit, vertical profiles of specific conductivity and temperature were measured at a main station defined as the deepest site in the lake. Both conductivity and temperature were determined at 0.5-m intervals in Fluevog and Peninsula lakes and at 0.25-m intervals in Oliva Lake from the surface to within 0.25 m from the lake bottom with a Hydrolab TC-2 meter. The trophogenic zone was defined as twice Secchi depth or to within 0.5 m of the lake bottom if Secchi depth was close to maximum lake depth. During ice-free periods, changes in lake volume were estimated by changes in water level recorded on a permanent marker in each lake. The lakes were hand-sounded in August 1983 to determine basin morphometry. Surface areas of the lakes were determined from 1 : 50 000 topographic maps and 1 : 5000 aerial photographs.

Water samples for analysis of phosphorus, nitrogen, and phytoplankton Chl *a* were collected on each visit from three stations per lake, including the main station. Integrated samples from the trophogenic zone were collected from the three stations with weighted Tygon tubing and pooled into one sample. Water samples were stored in Nalgene bottles as described in Prepas and Trew (1983) and were refrigerated prior to analysis. From March to September 1984, discrete samples for determination of dissolved oxygen (DO) were collected from the water column at the three stations with a 1.5-L aluminum drop-sleeve water bottle, at 0.5-m intervals from the lake surface to within 0.7 m of the lake bottom. The samples were stored in 50-mL glass-stoppered bottles and analyzed

within 2 h. Samples for determination of periphyton Chl *a* were collected monthly from April to September 1984: a 500-mL polyethylene collection bottle, squeezed to expel air and provide suction, was connected to a polyethylene tube that was moved over the surface of the lake sediments to suck up the top 2–3 cm of sediment and attached algae (Eaton and Moss 1966). Four to five samples were collected from each of two strata, a shallow stratum <0.5 m depth and a deep stratum >0.5 m depth, and the material was pooled to make one sample per stratum. Shallow sediments were collected directly from marked areas, while deeper sediments were collected with a four-barrel corer (Hamilton et al. 1970) and the top 2–3 cm of each core sampled. All collected material (sediment, periphyton, plus some lake water) was stored in 50-mL glass jars and refrigerated prior to analysis.

To estimate bacteria and zooplankton densities in the trophogenic zone, water samples were collected from 1 m below the surface of each lake. This depth was chosen as representative of the trophogenic zone. Bacteria were collected monthly from April to August 1984 at the main station with a 1.5-L water bottle; zooplankton were collected biweekly during the ice-free season at three stations with a 40-L Schindler-Patalas trap (Schindler 1969) fitted with an 80-μm Nitex net. For bacteria counts, 15 mL of water was placed in 20-mL polyethylene vials and preserved with 5 mL of 40% phosphate-buffered formalin prefiltered through a 0.45-μm Millipore membrane filter. Zooplankton were either stored in 75-mL Nalgene bottles for dry weight determination or preserved with chilled 2% formalin with 6% sucrose (Prepas 1978) in 10-mL glass vials for species identification and enumeration. Zooplankton gut contents were determined on one sampling date; 10 macrozooplankton of each species were anaesthetized with carbonated water prior to preservation (Haney and Hall 1973).

In 1984, primary production was determined biweekly at the main station in each lake. Water samples were collected from the appropriate depths, filtered through an 80-μm Nitex net to remove large zooplankton, and placed in 100-mL glass-stoppered light and dark bottles. Sets of two light and two dark bottles were suspended at 0.5-m intervals from 0.2 m below the lake surface to within 0.5 m of the lake bottom. Primary productivity was measured either as carbon uptake with inocula of 0.5–1.0 mL $NaH^{14}CO_3$ (1.5 $MBq \cdot mL^{-1}$) per bottle or as oxygen evolution. Incubations took place between 08:30 and 14:00 and lasted 3 or 4 h. Immediately after incubation the bottles were stored in a light-tight container for 1 h prior to laboratory analysis.

Laboratory Analysis

Within 48 h of collection, integrated water samples were analyzed for turbidity (Hach model 2100a turbidimeter), alkalinity (milligrams HCO_3-CO_3 per litre; potentiometric method of Environment Canada 1979), pH (Fisher Accumet digital pH meter), and specific conductivity (at 20°C; YSI model 31 conductivity bridge). Storage containers and glassware for chemical analyses were cleaned as in Bierhuizen and Prepas (1985). Glassware used in experiments with radioisotopes was soaked for 24 h in 2% Decon-75 (BDH Chemicals) and then cleaned as other glassware.

Water samples for phosphorus determination were analyzed as total phosphorus (TP; filtered through a 243-μm-mesh Nitex net), total dissolved phosphorus (TDP; filtered through a prerinsed 0.45-μm HAWP Millipore membrane filter) by the potassium persulfate method of Menzel and Corwin (1965) modified by Prepas and Rigler (1982), and soluble reactive phosphorus (SRP; filtered as for TDP) by the molybdenum blue method of Murphy and Riley (1962). All samples were filtered within 6 h of collection; TP and TDP determinations were made within 48 h and SRP determinations within 24 h. To determine whether a significant amount of particulate phosphorus could pass through the 0.45-μm filter size, replicate water samples were filtered through the 0.45-μm filters and 0.20-μm Nuclepore polycarbonate filters monthly from June to August 1984. Differences in dissolved phosphorus concentrations between TDP estimates averaged 0.5% with a maximum of 3.4%. The estimates were statistically indistinguishable for all lakes; probabilities for each lake were calculated for the difference between TDP estimates with the two filter sizes for each date (two-way ANOVA) then, since sample size was so small the probabilities were combined for all lakes with $\chi^2 = 3.24$, df = 6, $P > 0.75$ (Sokal and Rohlf 1981, box 18.1). TDP < 0.45 μm (henceforth simply TDP) thus accurately represents dissolved phosphorus in the lakes. While TP levels in the saline lakes reached 16 000 $\mu g \cdot L^{-1}$, the analytical technique for determination of phosphorus was nonlinear for TP levels >500 $\mu g \cdot L^{-1}$. Consequently, water samples from the saline lakes were diluted with double-distilled water (DDW) in a ratio of 1:10 for Fluevog and Peninsula lakes and 1:50 for Oliva Lake. Samples for nitrogen determination were analyzed as total Kjeldahl nitrogen (TKN) with the phenol-hypochlorite method of Solorzano (1969) and as nitrate–nitrite (NO_2–NO_3) with the cadmium–copper reduction method of Stainton et al. (1977), with techniques described in Prepas and Trew (1983). To be within the working range of the analytical techniques employed, water samples for TKN determination were diluted with DDW in ratios of 1:3 for Fluevog and Peninsula lakes and 1:5 for Oliva Lake. TN was calculated as the sum of TKN and NO_2–NO_3.

For phytoplankton Chl *a* determination, water samples were filtered through Whatman GF/C filters, frozen, and analyzed within 2 wk of collection by the ethanol extraction technique of Ostrovsky outlined in Bergmann and Peters (1980) with no phaeophytin correction. Ethanol extraction gives values statistically indistinguishable from Yentsch and Menzel's (1963) acetone extraction that corrects for phaeophytin (Prepas 1984). For phytoplankton species identification, 75 mL of the original sample was preserved with Lugol's solution and then observed under a Wild M40 inverted microscope. Within 48 h of collection, the periphyton samples were thoroughly mixed in the collection jars to produce a slurry and the volume recorded, and then a subsample was placed in a 20-mL culture tube with 10 mL of ethanol for 24 h. These samples were then placed in 50-mL plastic centrifuge tubes and spun for 10 min at 3200 rpm at 1500 × *g* Relative Centrifugal Force in an International Clinical Centrifuge model CL to separate the sediment and algal chlorophyll. The overlying water, dislodged algae, and chlorophyll were placed in 20-mL culture tubes and Chl *a* was measured as outlined for phytoplankton. To compare the relative importance of periphyton to phytoplankton, periphyton Chl *a* was first converted to an areal estimate (milligrams per square metre, stratum weighted) and then to a volumetric equivalent (micrograms per litre) assuming that the periphyton (micrograms per stratum) was mixed into the water overlying each stratum.

Samples for bacterial analysis were diluted with DDW in a ratio of 1:5 and filtered onto 0.20-μm Nuclepore polycarbonate filters. Samples were then enumerated within 2 wk of col-

lection by D. Bird (Department of Biology, McGill University, Montreal, Que.) with the epifluorescent DAPI stain method (Coleman 1980). To determine zooplankton dry weight, the sample volume was recorded and subsamples were filtered onto preweighed and predried Whatman GF/C filters within 12 h of collection. The filters were frozen for up to 2 wk, oven-dried at 60°C for 24 h, cooled in a desiccator, and weighed on a Cahn model G-2 electrobalance (similar to Gurtz et al. 1980). Zooplankton species were identified and enumerated in a modified Plexiglas Bogorov counting chamber (Gannon 1971) with a Wild M3 dissecting microscope. For abundant species, subsamples containing a minimum of 100 individuals were counted, while for rarer species the entire sample was counted.

Analysis of DO by the Winkler technique (Carpenter 1965) and analysis of ^{14}C primary productivity by the acid-bubbling technique (Schindler et al. 1972) were not suitable for this study, since the addition of acid to the saline water caused effervescence and loss of sample. DO was determined with the Miller method for inland saline waters (Walker et al. 1970). For Fluevog and Peninsula lakes, ^{14}C primary productivity was satisfactorily analyzed after filtration and acid-fuming (Lean and Burnison 1979); the relationship between filtered volume and isotope disintegrations per minute (DPM) was linear as long as a maximum 30 mL of inoculated sample was filtered. After filtration, the filters were fumed for 2 h in glass scintillation vials; then, 5 mL of Bray's scintillation fluor (Bray 1960) was added and the samples were counted on a Tracor Analytic Mark III 6881 liquid scintillation counter with an automatic quenching correction. For Oliva Lake, primary productivity was estimated by changes in DO; these changes were converted to carbon uptake with a photosynthetic quotient of 1.2 (Cole 1983). With both the ^{14}C and oxygen methods, primary productivity was calculated as light minus dark bottle readings. In Oliva Lake, ^{14}C primary productivity could not be determined, since biological uptake of carbon was obscured by high chemical uptake (>1500 mg $C \cdot m^{-3} \cdot h^{-1}$). Carbon uptake rates in Oliva Lake water "killed" with concentrated formalin were statistically indistinguishable from uptake rates in water that received no formalin (paired t-test: $t_{11} = 1.78$, $P > 0.10$). In Fluevog and Peninsula lakes, water samples killed with formalin had low chemical uptake rates of carbon (<20 mg $C \cdot m^{-3} \cdot h^{-1}$).

Orthophosphate uptake rates were determined in each lake with carrier-free $^{32}P\text{-}PO_4$ (New England Nuclear) five times over the periods from June to August 1983 and April to August 1984. For these assays, replicate experiments in which 1 mL of $^{32}P\text{-}PO_4$ (74 KBq $\cdot$ mL^{-1}) was added to 300 mL of lake water were run for 3–6 h at lakeside and for up to 4 d in the laboratory. The assay method of Lean and Rigler (1974) was slightly modified; Millipore Swinnex 25-mm disc filter holders fitted with 0.45-μm HAWP Millipore membrane filters were used for filtration. Filters with labelled lake water were placed in polyethylene scintillation vials, 5 mL of Bray's Fluor was added, and the samples counted within 48 h on the scintillation counter. The $^{32}P\text{-}PO_4$ tracer batch was assessed in uptake experiments with water from two freshwater lakes in Alberta; orthophosphate turnover rates were rapid (as previously reported by Prepas 1983), indicating that the tracer was available for algal uptake. Laboratory bioassays to determine factors limiting algal growth in the study lakes were run with water collected from the trophogenic zone; all experiments were repeated twice with three to four replicates for each control and experimental treatment. Lake water filtered through 0.45-μm filters, together with an unfiltered inoculum of native algae plus the bioassay treament, was placed in 250-mL Erlenmeyer flasks beside a window that received full sunlight. Samples were shaken twice daily to prevent algal sedimentation and incubated for 2 wk prior to Chl *a* analysis. Phosphorus, inorganic nitrogen, and general nutrient and iron limitation were tested by additions of KH_2PO_4 in phosphorus levels double the TP concentrations in the lake controls, either KNO_3 or NH_4Cl in nitrogen levels 1.5, 2, and 4 times the TN concentrations in the controls, soil extract solution (prepared by autoclaving garden soil in DDW; Carmichael and Gorham 1974) in levels of 20 mL of soil extract per litre of lake water, and EDTA (Shubert 1978) in levels of 0.2 and 0.4 m*M* per flask, respectively.

Zooplankton grazing experiments were performed twice from June to August 1984 in Fluevog and Oliva lakes. For these experiments, water was collected from 0.2 m below the lake surface and filtered through an 80-μm Nitex net into 100-mL glass-stoppered bottles. In the two experimental bottles, large grazers (cladocerans and copepods in Fluevog Lake and *Artemia* in Oliva Lake) were added in densities equal to those in the lake the previous week, while no zooplankton were added to the two control bottles. The bottles were suspended at 0.2 m below the lake surface for 2 h. The short incubation time would minimize bacterial build up and was calculated to be sufficient to see a measurable effect on algal Chl *a* levels with the zooplankton densities used. After incubation, samples were preserved with 1 mL of concentrated formalin and analyzed for Chl *a*. Addition of formalin did not interfere with Chl *a* analysis; in a laboratory test, Chl *a* readings were similar for samples with and without formalin (unpaired t-test: $t_{14} = 0.48$, $P = 0.64$).

Data Manipulations

Mean growing season (May–September) phosphorus, nitrogen, and phytoplankton Chl *a* levels were calculated as averages of the integrated samples collected from the trophogenic zone. Mean growing season rates of primary productivity (V) were calculated from daily values which were volume weighted over the trophogenic zone. Whole-lake conductivity estimates were calculated from data from discrete samples, volume weighted over the water column. Measured mean growing season Chl *a* and V values were compared with values predicted by the empirical models of Smith (1979, 1982), the former model based on TP, Chl *a*, and V data from 49 freshwater lakes and the latter based on TP, TN, and Chl *a* data from 127 freshwater lakes. Measured summer densities of bacteria were compared with those predicted by Bird and Kalff's (1984) model based on bacteria and Chl *a* data from 39 freshwater, marine, and estaurine systems. Measured mean growing season zooplankton biomass was compared with that predicted by McCauley and Kalff's (1981) model based on zooplankton and phytoplankton biomass data from 17 freshwater lakes. Zooplankton dry weight and Chl *a* were converted to wet weight and phytoplankton biomass, respectively, as suggested by McCauley and Kalff (1981). Ninety-five percent confidence limits for points outside the regression data sets were calculated about predicted Chl *a* and V values with data from Smith (1979) and V. H. Smith (University of North Carolina, unpubl.); 50% confidence limits were used where measured values were far outside the original data set, as in Chl *a* levels predicted from TP (Smith 1979), or where predicted and mea-

TABLE 2. 1984 mean growing season total phosphorus (TP), total dissolved phosphorus (TDP), and total nitrogen (TN) levels in the trophogenic zone of the study lakes.

Lake	TP ($\mu g \cdot L^{-1}$)	TDP ($\mu g \cdot L^{-1}$)	TN ($\mu g \cdot L^{-1}$)	TN:TP
Fluevog	2 310	2 165	3 923	1.7
Peninsula	3 658	3 502	4 178	1.1
Oliva	13 304	12 817	11 517	0.9

sured values were similar, as in V values predicted from Chl *a* (Smith 1982). Similar 95% confidence limits were calculated about predicted bacteria densities with information from Bird and Kalff (1984), and about McCauley and Kalff's (1981) phytoplankton–zooplankton relationship from Prepas (1984).

Statistical analyses followed Snedecor and Cochran (1980) and Sokal and Rohlf (1981) and were performed with BMDP statistical software on the Amdahl computer 580/5860 at the University of Alberta. Data collected in 1983 were similar to those collected in 1984 unless otherwise stated.

Results

Chl *a*, Primary Productivity, and Nutrient Levels

Mean growing season TP, TDP, and TN levels were extremely high in all three study lakes: TP and TN varied from 2300 to over 11 500 $\mu g \cdot L^{-1}$ and TDP from 94 to 96% of TP. TN:TP ratios (by weight) were low, ranging from 0.9 to 1.7 (Table 2). Despite the extremely high TP and TN levels, mean growing season phytoplankton Chl *a* levels were extraordinarily low in all the lakes (≤ 10 $\mu g \cdot L^{-1}$; Table 3). Periphyton Chl *a* levels were also low (mean areal estimates ≤ 72 $mg \cdot m^{-2}$ and mean volumetric equivalents ≤ 50 $\mu g \cdot L^{-1}$; Table 3). With no phaeophytin correction, measures of periphyton Chl *a* represent maximum Chl *a* levels in the sediments. In Oliva Lake, periphyton was considerably more abundant than phytoplankton (50 compared with 4 $\mu g \cdot L^{-1}$), whereas in the other two lakes, the two algal communities were of similar size. However, even the combined phytoplankton and periphyton Chl *a* levels (17, 18, and 54 $\mu g \cdot L^{-1}$ for Fluevog, Peninsula and Oliva lakes, respectively) were very low relative to TP and TN levels. The measured Chl *a* levels were compared with predicted levels based on TP and TN levels and Smith's (1982) empirical model. The measured phytoplankton Chl *a* levels were <2% of the predicted levels and the combined periphyton and phytoplankton Chl *a* levels were <5% of the predicted values (Table 3), well outside the 50% confidence limits for the predicted values. Therefore, the combined phytoplankton and periphyton communities were not large enough to use a major portion of the nutrient pool.

Measured mean growing season rates of phytoplankton primary productivity (V) in the lakes varied from 17 to 156 $mg\ C \cdot m^{-3} \cdot d^{-1}$ (Table 4). Measured V values were similar to predicted values based on measured phytoplankton Chl *a* and Smith's (1979) empirical model. In contrast, the measured V values were 3–4 orders of magnitude less than predicted values based on TP levels and Smith's (1979) model, and fell outside the 95% confidence limits for the predicted rates (Table 4). Mean phytoplankton primary productivity to Chl *a* ratios for the growing season were 11, 16, and 4 for Fluevog, Peninsula, and Oliva lakes, respectively, and were comparable with productivity to Chl *a* ratios for other saline and freshwater lakes (Hammer 1981; Wetzel 1983). Therefore, phytoplankton were not turning over unusually fast in the study lakes.

$^{32}P\text{-}PO_4$ uptake was not detectable in any of the study lakes; orthophosphate turnover times were very long, approaching $+\infty$ (Lean and Rigler 1974), and thus biologically available phosphorus was abundant in the lakes. In all the lakes, >80% of summer TP was SRP. In contrast, in freshwater lakes (TDS <500 $mg \cdot L^{-1}$) in central Alberta which cover a spectrum of depths and productivity levels, 1–42% of summer TP was SRP (Prepas 1983). In bioassays with the saline lake waters, the additions of KH_2PO_4 did not increase Chl *a* levels over control levels (split-plot ANOVA to test treatment effects, with lakes and treatments as groups and experiment dates as subplots: $F_{1,12} = 0.36$, $P = 0.27$). Additions of KNO_3 in nitrogen concentrations 1.5, 2, and 4 times TN concentrations in the lakes increased Chl *a* levels by an average of 12, 7, and 18 times, respectively, over control levels in all lakes. Additions of NH_4Cl in nitrogen concentrations 1.5, 2, and 4 times TN concentrations in the lakes increased Chl *a* levels by an average of 5, 7, and 10 times, respectively, over control levels. In one experiment with Fluevog Lake water, additions of NH_4Cl at the "4 times" level caused no significant change in Chl *a* levels from control levels (a posteriori Dunnett's test with total MS_{error} from split-plot ANOVA: $P > 0.05$). In the 17 other cases, addition of inorganic nitrogen significantly increased Chl *a* over control levels (Dunnett's test: $P < 0.05$ for all lakes, treatments, and dates). Variability in Chl *a* levels among flasks was greatest with the highest additions of inorganic nitrogen (i.e. the "4 times" addition level). Additions of soil extract caused no increase in Chl *a* in any of the experiments (split-plot ANOVA: $F_{1,12} = 0.53$, $P = 0.48$). Additions of EDTA caused no increases in Chl *a* levels in either Fluevog or Peninsula Lake water (Dunnett's test with total MS_{error} from split-plot ANOVA: $P > 0.05$), but both the 0.2 and 0.4 mM additions of EDTA significantly increased Chl *a* levels in Oliva Lake water (Dunnett's test: $P < 0.05$) by an average of 1.4 and 2 times, respectively, over control levels. Thus, only inorganic nitrogen was consistently limiting to algal growth in all the lakes, while there was evidence of iron limitation in Oliva Lake. Phytoplankton species present in all bioassay experiments, mainly *Microcystis aeroginosa* in Fluevog and Peninsula Lake water and various small diatoms in Oliva Lake water, were species found naturally in the lakes.

Bacteria and Zooplankton

Pelagic bacterial densities in the study lakes ranged from 1.2×10^7 to 2.3×10^7 $cells \cdot mL^{-1}$. These densities are 2–8 times higher than predicted densities based on phytoplankton Chl *a* levels and Bird and Kalff's (1984) empirical model (Table 5) and outside the 95% confidence limits about the predicted values, except for Peninsula Lake. Most bacteria in the study lakes were smaller than bacteria in freshwater lakes (0.40-μm diameter as compared with 0.60 μm; D. Bird, pers. comm.). Total bacteria numbers in the lakes were probably underestimated, since bacteria in the lake sediments were not sampled. Zooplankton were also abundant in the lakes; mean growing season zooplankton dry weights were 1.3, 1.4, and 8.2 $mg \cdot L^{-1}$ in Fluevog, Peninsula, and Oliva lakes, respectively. Zooplankton wet weight in each lake was an order of magnitude higher than that predicted from measured phytoplankton biomass and McCauley and Kalff's (1981) empirical model (Fig. 1). Hence, both bacteria and zooplankton populations were larger than expected from the size of the phyto-

TABLE 3. Comparison of 1984 measured mean growing season phytoplankton and periphyton chlorophyll (Chl *a*) in the study lakes with predicted phytoplankton Chl *a* based on measured total phosphorus (TP) and total nitrogen (TN) and Smith's (1982) empirical model.

Lake	Phytoplankton Chl *a* ($\mu g \cdot L^{-1}$)	Periphyton Chl *a* ($mg \cdot m^{-2}$)	Periphyton Chl *a* ($\mu g \cdot L^{-1}$)	Predicted Chl *a* ($\mu g \cdot L^{-1}$)	50% confidence limits
Fluevog	3	19	14	450	80–2 600
Peninsula	10	17	8	700	90–4 980
Oliva	4	72	50	2500	180–35 360

TABLE 4. Comparison of 1984 measured mean growing season primary productivity (*V*) in the trophogenic zone of the study lakes with productivity predicted from measured phytoplankton chlorophyll (Chl *a*) or total phosphorus (TP) and Smith's (1979) empirical models.

Lake	*V* observed ($mg\ C \cdot m^{-3} \cdot d^{-1}$)	*V* predicted from Chl *a* ($mg\ C \cdot m^{-3} \cdot d^{-1}$)	50% confidence limits	*V* predicted from TP ($mg\ C \cdot m^{-3} \cdot d^{-1}$)	95% confidence limits
Fluevog	32	31	0–132	23 950	22 100–25 780
Peninsula	156	176	80–270	37 960	35 970–40 880
Oliva	17	48	0–149	138 280	134 590–148 970

TABLE 5. Comparison of 1984 measured mean summer bacterial densities at 1 m below the lake surface in the study lakes with densities predicted from mean summer phytoplankton chlorophyll (Chl *a*) and Bird and Kalff's (1984) empirical model.

Lake	Observed bacteria (10^6 cells $\cdot mL^{-1}$)	Predicted bacteria (10^6 cells $\cdot mL^{-1}$)	95% confidence limits
Fluevog	12	2	0.8–5.0
Peninsula	13	6	4.0–15.0
Oliva	23	3	1.0–7.0

plankton standing crop.

To evaluate whether algal and bacterial biomass in the lakes was sufficient to support the zooplankton populations, daily carbon requirements of zooplankton were compared with carbon mass in the algae and bacteria. For minimum population growth, zooplankton populations in the lakes require 1.1, 1.2, and 6.5 mg $C \cdot L^{-1}$ daily in Fluevog, Peninsula, and Oliva lakes, respectively. These calculations assume that each 25 µg dry weight of zooplankton requires 0.02 mg $C \cdot d^{-1}$ after Lampert (1977) who worked with 25-µg (dry weight) *Daphnia pulex*, and that data based on *D. pulex* can be applied to the total zooplankton community. Combined phytoplankton and periphyton carbon levels in the study lakes (carbon mass = 10 × Chl *a*; Frost 1972) were estimated at 0.17, 0.18, and 0.54 mg $C \cdot L^{-1}$, whereas carbon levels of bacteria populations (400 mg $C \cdot cell^{-1}$; Overbeck 1980) were estimated at 0.48, 0.52, and 0.92 $\mu g \cdot L^{-1}$ in Fluevog, Peninsula, and Oliva Lakes, respectively. Thus, algal populations in the saline lakes could supply only 8–16% of the carbon requirements for the zooplankton populations, while combined algal and bacteria populations would supply 22–60% of carbon requirements. For freshwater lakes in Alberta that cover a wide range of productivities (Prepas and Trew 1983; A. Trimbee and E. E. Prepas, University of Alberta, unpubl.), calculations indicate that mean summer phytoplankton populations would supply 61–84% of daily zooplankton carbon requirements and combined mean summer phytoplankton and bacteria populations would supply 140–600% of carbon requirements. Phytoplankton, a major food source for zooplankton in freshwater lakes, is thus insufficient to support the large zooplankton populations in the saline study lakes. Therefore, bacteria and detritus are likely an important zooplankton food source in the study lakes. This conclusion is supported by observations of zooplankton gut contents: in Oliva Lake, *Artemia salina* were feeding primarily on brown material (bacteria and detritus), while in Fluevog and Peninsula lakes, *Daphnia similis* and *Diaptomus sicilis* were feeding equally on brown material and

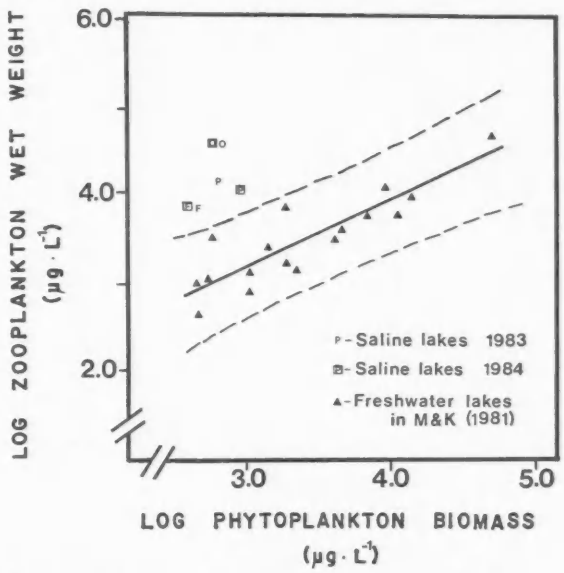

FIG. 1. 1983 and 1984 log mean growing season zooplankton wet weight at 1 m below the lake surface related to log phytoplankton biomass in the trophogenic zone in the three saline lakes (F = Fluevog, P = Peninsula, O = Oliva) and data from 17 temperate freshwater lakes analyzed by McCauley and Kalff (M & K) (1981). Solid line represents McCauley and Kalff's model; broken lines are 95% confidence limits for predicted values outside the model.

green algal cells.

Despite the relatively high densities of zooplankton in the saline lakes, results from field experiments indicated that zooplankton grazers do not have a substantial effect on phytoplankton population growth. Phytoplankton Chl *a* levels were statistically indistinguishable in bottles with and without grazers in both Fluevog and Oliva lakes (split-plot ANOVA to test treatment effects, with lakes and treatments as groups and experiment dates as subplots: $F_{1,4} = 2.52$, $P = 0.17$).

Discussion

It is clear from this study that the extraordinarily high concentrations of TP and TN in the study lakes are not effectively utilized by the algal communities. Phytoplankton and periphyton Chl *a* and phytoplankton primary productivity were all much lower than would be predicted from ambient nutrient levels and empirical models developed for freshwater lakes. Freshwater nutrient–productivity relationships thus do not appear to be valid for these prairie saline systems.

TP is definitely not limiting algal growth in the saline lakes, in contrast with many freshwater lakes. The negligible orthophosphate uptake rates and the high SRP levels (a good measure of orthophosphate in lakes with low orthophosphate turnover times; Peters and MacIntyre 1976) in the study lakes, combined with the lack of increased algal growth in bioassays spiked with KH_2PO_4, suggest that biologically available phosphorus is abundant and in quantities well above short-term algal requirements. TP may be acting as a conservative rather than a dynamic element in the study lakes; concentrations could then be related primarily to physical processes in the lakes. Seasonal changes in TP in the study lakes were associated with changes in lake volume: observed TP levels were not significantly different from levels calculated from a constant TP mass (determined for August 1983) corrected for changes in lake volume (paired *t*-test: $P > 0.20$ for all the lakes). As well, seasonal changes in TP levels and marker height above the lake surface (a measure of lake volume) were highly correlated (Fluevog $r = 0.92$, $n = 12$, $P = 0.001$; Peninsula $r = 0.64$, $n = 12$, $P = 0.02$; Oliva $r = 0.77$, $n = 14$, $P = 0.001$). Aeolian loadings (14 mg TP·m^{-2} for the open water season; from Riley and Prepas 1984) supplied only a very small portion of the measured TP in the water column. These results support the idea that allochthonous input of TP was minimal and that lake TP concentrations were affected by physical rather than biological processes.

TN is also not limiting to algal growth in the study lakes, based on the extremely high Chl *a* levels predicted from measured TN and TP levels and Smith's (1982) model. However, TN in prairie saline lakes may not be a good indicator of biologically available nitrogen. Algal growth appeared to be limited by inorganic nitrogen: in the laboratory bioassays, Chl *a* levels were markedly increased when KNO_3 and NH_4Cl were added, although these Chl *a* levels were still lower than levels expected from the ambient TN and TP concentrations. Addition of general nutrient solution failed to promote algal growth in any of the lake bioassays; nitrogen levels in the soil extract inoculum were relatively low (265 μg TN·L^{-1}). The high levels of inorganic nitrogen needed to stimulate algal production in bioassay experiments suggest that nitrogen cycling may be different in these saline lakes as compared with freshwaters. In these prairie saline lakes, inorganic nitrogen might be a useful indicator of biologically available nitrogen. High pH levels in the study lakes may render much of the ammonia unavailable. At a pH above 9.0, as recorded in the three lakes, 30% of the measured ammonia would be present as toxic un-ionized ammonia (NH_3) (Trussell 1972). High toxic ammonia levels might explain decreased algal growth in some bioassays with Fluevog Lake water when high levels of NH_4Cl were added (i.e. the "4 times" addition level). Inorganic nitrogen limitation has been proposed in other saline lake studies, either from algal bioassays (Moss 1969; Stephens and Gillespie 1976) or from correlations between inorganic nitrogen levels and phytoplankton Chl *a* (Haertl 1976).

Iron limitation was detected only in Oliva Lake where additions of EDTA increased algal growth, a result similar to that observed in saline Devil's Lake, North Dakota (Shubert 1978). High pH levels in Oliva Lake (9.9) could reduce iron solubility (Stumm and Morgan 1981). EDTA can chelate metals other than iron, however, so the possibility of algal limitation by other ions cannot be ruled out.

The high salinity of the three study lakes could influence algal productivity: some micronutrients might be less available or algal cells may suffer from extreme osmotic stress (Por 1980). The ratio of specific ions could also influence productivity. The unproductive saline lakes in Alberta are dominated by Na^+, SO_4^{2-}, and CO_3^{2-} (Bierhuizen and Prepas 1985), as compared with freshwater lakes in Alberta that are dominated by Ca^{2+} and HCO_3^{2-} (Alberta Environment, unpubl.). The ions Mg^{2+} and SO_4^{2-} are relatively more important in the saline lakes in western Canada (Topping and Scudder 1977; Barica 1978; Hammer 1978; Bierhuizen and Prepas 1985) than in saline lakes in other parts of the world, e.g. East Africa (Talling and Talling 1965), the western United States (Anderson 1958; Wetzel 1964; Armstrong et al. 1966), and Australia (Bayly and Williams 1966). Outside of western Canada, some saline lakes can be extremely productive with phytoplankton Chl *a* levels > 500 μg·L^{-1} despite TDS > 5000 mg·L^{-1} (Melack and Kilham 1974 in East Africa; Armstrong et al. 1966 and Walker 1975 in the western United States; Hammer 1981 in Australia). Periphyton Chl *a* levels > 300 mg·m^{-2} have been reported for saline lakes in the western United States. (Castenholz 1960; Wetzel 1964). Although the major difference between the unproductive saline lakes of western Canada and productive saline lakes elsewhere appears to be the relative importance of Mg^{2+} and SO_4^{2-}, the effects of specific ion ratios on algal growth need further investigation.

Some of the low algal productivity in the Alberta saline lakes may be explained by biological interactions with bacteria and zooplankton. In the study lakes, bacterial densities were high relative to the phytoplankton Chl *a* levels and to bacterial densities in freshwater lakes (Bird and Kalff 1984) although similar to densities reported for other saline lakes (Mason 1967; Kilham 1981). The bacteria in the study do not seem to be competing with algae for orthophosphate (low ^{32}P-PO_4 uptake rates in the lakes incorporate both bacterial and algal uptake), but they may compete with algae for other nutrients. The abundant bacteria may support large protozoan populations as well, although this was not investigated. Such high bacterial densities require a large amount of organic substrate. Allochthonous input of organic material was low (C. E. Campbell, pers. obs.). Groundwater input and resuspension of bottom sediments would provide some organic material. As well, the high density of the saline water, with conductivity–density gradients in Oliva Lake, may inhibit sinking of organic debris to the

sediments.

Zooplankton biomass in the study lakes was also extremely high relative to phytoplankton Chl *a* levels, so zooplankton could exert considerable grazing pressure on the algal populations. Field experiments did not indicate particularly heavy zooplankton grazing pressure on phytoplankton. Zooplankton grazing was probably heaviest on bacteria (and possibly protozoa) which were relatively more abundant than phytoplankton. In contrast, in other saline lakes with zooplankton densities similar to those reported in this study, removal of grazers from containers resulted in increased algal growth although these observations were not supported by statistical analyses (Anderson 1958; Mason 1967). However, these other grazing experiments were allowed to run for an average of 124 h (Anderson 1958) and 120 d (Mason 1967) and thus are difficult to compare with the 2-h experiments in this study. Container experiments of long duration may not reflect natural population dynamics. Field observations from other studies also suggest that zooplankton in saline lakes, particularly *Artemia salina*, can decrease algal standing crop in small saline systems (Por 1980; Javor 1983). In Oliva Lake, even with low winter light levels under the ice from January to March 1984, mean phytoplankton Chl *a* levels did increase slightly to 7.4 $\mu g \cdot L^{-1}$ as *Artemia* populations disappeared. The increase was remarkably modest relative to ambient TP and TN levels. In Fluevog and Peninsula lakes, similar winter decreases in zooplankton populations were not mirrored by increases in Chl *a* levels, which suggests that grazing pressure had no detectable effect on algal populations. Even in the absence of zooplankton grazers, such as in the field experiment and the laboratory bioassays, Chl *a* levels did not increase to the extraordinarily high levels that would be expected from the TP and TN levels in the water. Some other inhibitor of algal growth, possibly chemical, is thus implicated. To determine the precise impact of grazers in prairie saline lakes, zooplankton grazing rates need to be studied in greater detail.

Thus, the cycling of organic material within the biological community in these prairie saline lakes may differ from that observed in freshwater lakes. Algal biomass is a relatively small part of the total biomass of the saline lakes, in contrast with the freshwater lakes in this region, and is insufficient to maintain the existing zooplankton populations. Consequently, abundant bacteria and detritus are probably an important food source for zooplankton grazers in the saline lakes (observed for *Artemia salina* in Solar Lake, Sinai; Cohen, reported in Por 1980), as is occasionally true in some oligotrophic freshwater lakes (Gulati 1975).

The low algal productivity of the saline study lakes thus appears to be influenced by some aspect of the high salinity which renders the algae unable to take advantage of the high nutrient levels. Physiological inhibitions due to the relative concentrations of Mg^{2+} and SO_4^{2-} need to be examined.

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Exclusion of Adult Alewife, *Alosa pseudoharengus*, Using Low-Frequency Sound for Application at Water Intakes

Gerard T. Haymes and Paul H. Patrick

Ontario Hydro Research Division, 800 Kipling Avenue, Toronto, Ont. M8Z 5S4

Haymes, G. T., and P. H. Patrick. 1986. Exclusion of adult alewife, *Alosa pseudoharengus*, using low-frequency sound for application at water intakes. Can. J. Fish. Aquat. Sci. 43: 855–862.

Experiments to test the effectiveness of low-frequency, high-intensity sound in excluding alewife, *Alosa pseudoharengus*, from an experimental net structure were conducted on Lake Ontario near Pickering, Ont. Sound was generated by modified seismic devices called pneumatic poppers. The number of alewife entering the experimental structure was reduced by 71–99% when the poppers were operating. Sonar evidence from one test suggested that another species which was not caught in the collection nets was less influenced by the acoustic deterrent. The results suggest that low-frequency, high-intensity sound may be effective in reducing losses of adult alewife at water intakes.

On a réalisé des expériences visant à vérifier l'efficacité d'un son de basse fréquence mais de forte intensité pour écarter des gaspareaux (*Alosa pseudoharengus*) d'une structure expérimentale faite en filet sur le lac Ontario près de Pickering (Ontario). Le son a été produit par des dispositifs sismiques modifiés appelés résonateurs pneumatiques. Le nombre de gaspareaux pénétrant dans la structure expérimentale a été réduit de 71 à 99 % quand les résonateurs étaient en opération. Des indications par sonar provenant d'un test donnent à penser qu'une autre espèce qui n'avait pas été capturée dans les filets de collecte était moins influencée par l'effet acoustique dissuasif. Les résultats portent à croire que le son de basse fréquence et de forte intensité peut être efficace pour réduire les pertes de gaspareaux adultes au niveau des prises d'eau.

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Exploitation of fish behavior for managing fish at water intakes has recently received considerable interest (Hocutt 1980; Haymes et al. 1984; Patrick et al. 1985; Sager et al. 1985). Behavioral systems rely on the voluntary responses of fishes to a controlled stimulus, such as light or sound, to reduce fish losses due to passage through turbines or impingement on intake screens. These systems are preferred to physical barriers, such as fine-mesh screens installed upstream of an intake, because they cost less and have limited potential for fouling.

The alewife, *Alosa pseudoharengus*, is a major species impinged on screens at thermal generating stations employing once-through cooling systems on the Great Lakes. Alewife are also lost at generating facilities on rivers of northeastern United States and eastern Canada draining into the Atlantic Ocean. To reduce losses of alewife at generators, an effective means of excluding this species from water intakes is required.

The majority of studies on the hearing abilities and response to sounds of clupeids has been conducted on Atlantic herring, *Clupea harengus harengus* (e.g. Enger 1967; Blaxter and Hoss 1981; Blaxter 1985). These studies suggest that clupeids can hear sounds over a wide frequency range and are capable of directional hearing. Negative behavioral responses by Pacific herring, *C.h. pallasi*, have been demonstrated for a variety of sounds including those generated by boats and fishing gear (Schwarz and Greer 1984). The potential for application of acoustics in fisheries management has been reviewed by Tavolga (1980) and a bibliography of early work on the effects of sound on fish has been compiled by Moulton and Backus (1955).

The purpose of this study was to determine whether alewife could be excluded from an experimental structure using low-frequency, high-intensity sound as a behavioral deterrent.

Materials and Methods

Sound Stimulus

Sound was generated by pneumatic poppers (Bolt Technology, Norwalk, CT), modified seismic devices which emit a low-frequency, high-intensity sound when fired underwater with high in-line air pressure. The pulses are broad band (20–1000 Hz) with most of the energy at a fundamental frequency of approximately 60 Hz (Fig. 1b). The acoustic signal consists of a rapid peak (2 ms in duration) followed by a low sinusoidal ringing which persists for approximately 150 ms (Fig. 1a).

Study Apparatus

Field tests of the effectiveness of pneumatic poppers in excluding alewife were conducted at the Pickering diversion test system situated in Lake Ontario, approximately 25 km east of Toronto. The diversion system is 78 m offshore from the surface intake of the Pickering Nuclear Generating Station (Fig. 2).

The diversion system consists of two structures; the west

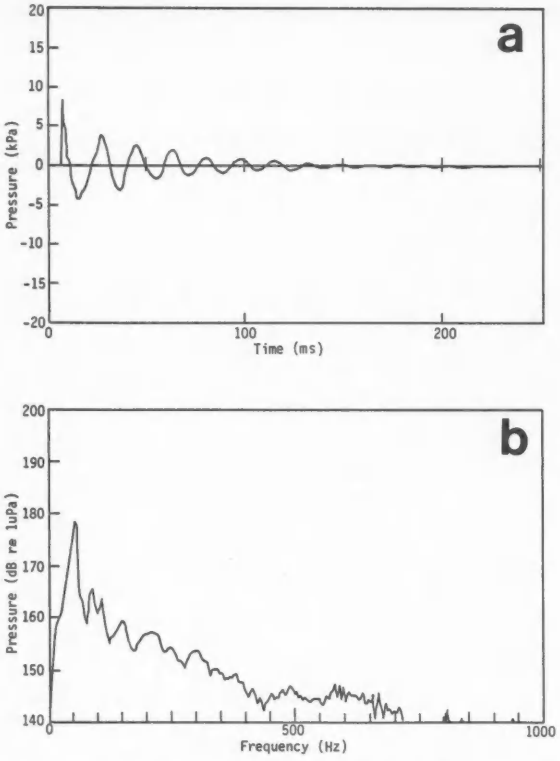


FIG. 1. (a) Time history and (b) frequency spectrum of the acoustical signal measured at 1 m distance from a single popper at 3 m depth.

structure (experimental) was fitted with 12 pneumatic poppers and a rope net (1983 only), while the east (nontreatment) structure was not fitted with poppers or a rope net. Each structure was approximately 9 m wide and intersected the entire water column (approximately 6 m).

Each structure comprised nine 0.3-m pilings arranged in three rows (Fig. 3). Each of the four pilings in the middle row on the experimental structure supported three pneumatic poppers. The two north pilings of both the experimental and east structures supported frame nets (3.8-cm-mesh gill net, effective in capturing adult alewife, in a metal frame) which collected fish passing through the structure. The three south pilings of the experimental structure supported a rope net in 1983 and were not used in 1984.

The rope net barrier consisted of two 3.9-m-wide by 6.7-m-high panels constructed of 2.5-cm nylon rope. The vertical components of the barrier consisted of two fused ropes presenting a 5-cm surface. Single horizontal ropes were attached to the vertical components to produce 15-cm^2 spacings between the ropes. Although alewife could easily pass through these openings, studies by P. H. Patrick and R. W. Sheehan (in prep.) indicated that this spacing was effective in excluding the majority of alewife encountering it. The rope net could be raised and lowered as required.

A single air hose ran along the lake bottom from either an 11.8-L·s^{-1} Ingersoll-Rand heavy duty compressor (1983) or a 3.4-L·s^{-1} Bauer compressor with a series of four compressed air storage bottles (1984) situated on the west groin to a manifold on the experimental structure. Twelve air hoses ran from the manifold to the pneumatic poppers. Tests were run at in-line pressures ranging from approximately 17 to 21 MPa in 1983 and 12 to 21 MPa in 1984. All poppers fired together approximately 15 times per minute.

Experimental Procedure

From mid-July to mid-August when alewife are relatively abundant in nearshore waters (Graham 1956), 2-h tests were conducted during the day and night in 1983 and during the night only in 1984. Day tests conducted during 1983 are not included in this report, as the number of alewife in the area of the test system was too low for statistical analysis. In 1983, tests were run with 12 poppers operating with and without the rope net deployed and with the rope net alone, and in 1984 tests were run with 1, 2, 4, 6, 8, and 12 poppers operating without the rope net deployed. Control tests were run with no poppers operating.

In addition to the collection nets on the structures a 15.2-m-long by 2-m-high 3.8-cm-mesh gill net panel was set to the east and west of the structures (wing nets) to verify the presence of alewife in the test area. At the end of a test, all of the nets were lifted and the number, species, and direction (i.e. moving inshore or offshore) of fish caught in the nets were noted.

An effectiveness index (E) was defined as the difference between the catch in the experimental structure during an experimental test (C_{exp}) and in the experimental structure during a control test on the same night (C_{con}), as a percentage of C_{con}:

$$E = 100(C_{exp} - C_{con})/C_{con}$$

When a control test was not conducted on the same night as an experimental test, the paired C_{con} was defined as the average of the catches in the experimental structure resulting from the earliest control tests conducted prior to and following that experimental test. Although it was originally intended to use the catch in the east structure for comparison with the experimental catch, poppers on the experimental structure reduced the catch on the east structure.

Statistical comparisons of the results utilized parametric statistics. As the variation in the catch records of alewife appeared to be proportional to the means, the data were log-transformed (Snedecor and Cochran 1967). The effectiveness indices were subjected to an arcsin square root transformation before statistical analysis, as their distribution was skewed toward 100% (Snedecor and Cochran 1967).

Acoustic measurements were taken at 3 m depth along a transect running perpendicular from each of the experimental and east structures. They were taken once at 1, 2, 4, 8, 16, and 32 m from each structure for each of 1, 2, 4, 8 (1984), and 12 (1983) poppers. The acoustic measuring system consisted of a Chesapeake SH101A hydrophone connected by a 20-m cable to a preamplifier (General Radio "Sound and Vibration Analyzer" type 1564-A). The data were recorded on a Nagra III tape recorder and run through a Nicolet 446A FFT analyzer.

For several of the tests conducted in 1984 an acoustic fish counting system was employed to monitor the relative abundance of fish in front of the experimental structure and their response to the poppers. The system consisted of a modified transceiver and transducer (Edo Western Corp., models 248 and 6203), time-varied gain receiver (Ithaco, model 94352), a fibre-optic graphic recorder (Honeywell Inc., model 1856A), and an echo analysis control subsystem (Eda Instruments, Toronto). The transducer was fixed to an anchored frame at middepth and directed toward the experimental structure from

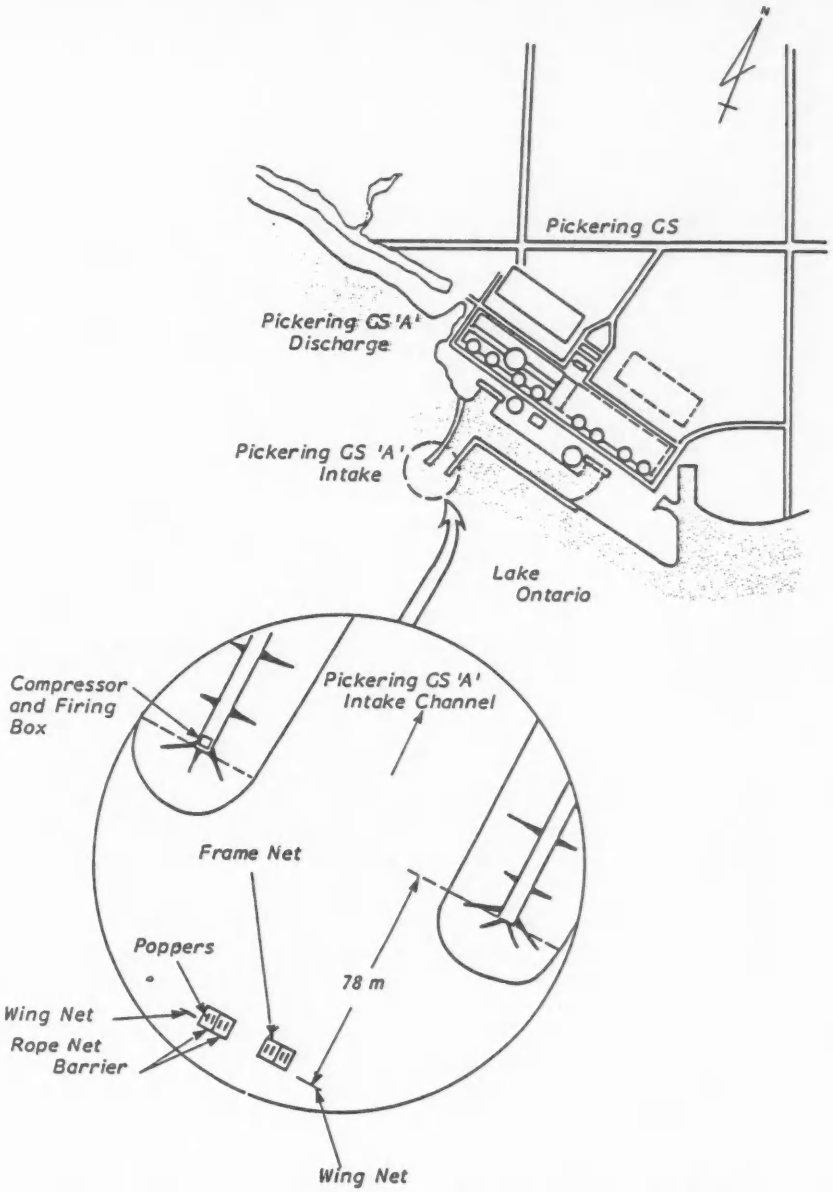


FIG. 2. Location of the fish diversion test system in Lake Ontario at the Pickering Nuclear Generating Station.

a distance of approximately 25 m.

Results

Acoustic Measurements

Acoustic measurements taken in front of the structures indicated that despite a lower operating pressure at the time of measurement in 1984 (17.5 MPa) than in 1983 (21.7), the acoustic pressures measured for 8 poppers in 1984 (2.3–23.9 kPa) were greater than those measured for 12 poppers in 1983 (0.5–9 kPa, Table 1). This difference was attributed to slight modifications to the poppers made by the manufacturer in 1984. Acoustic pressures at distances greater than 2 m from the experimental structure increased with the number of poppers operating (one to eight poppers). Acoustic pressures measured in front of the east structure also increased with the number of poppers employed, ranging from 0.2–0.4 kPa for one popper to 1.0–1.4 kPa for eight poppers. The fundamental frequencies generally ranged from 50 to 60 Hz in front of the experimental structure but were even more variable in front of the east structure where acoustic pressures were much lower.

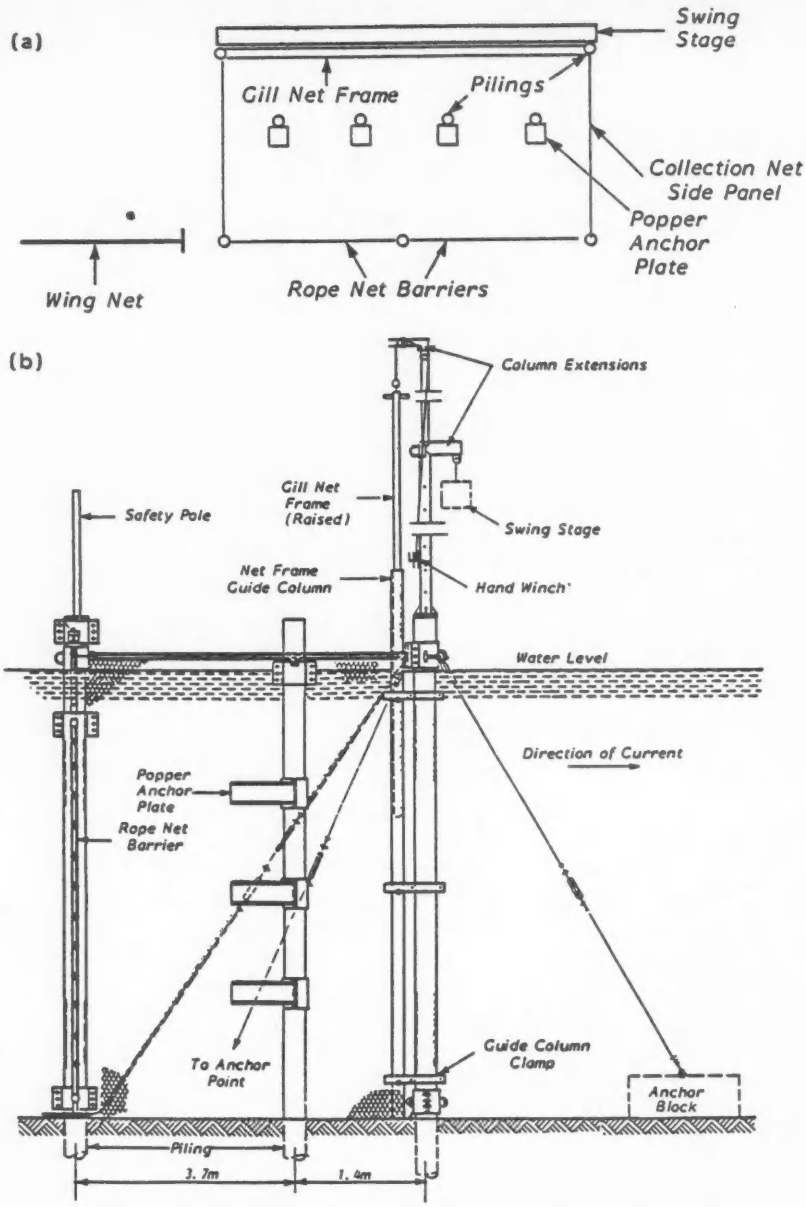


FIG. 3. (a) Top and (b) side views of the experimental structure of the fish diversion test system.

Exclusion Tests

All but 8 of the 26 340 fish collected during our tests were adult alewife. Catches in the frame nets were highly variable with standard deviations for some treatments approaching or exceeding the means (Table 2). The mean catches of alewife moving inshore in the experimental structure when poppers and/or the rope net were employed were consistently lower than those in paired control tests. Furthermore, except for one rope net test, the catch of alewife, moving inshore, in the experimental frame net was always lower than that in the east frame net in individual tests. Similarly, the mean catches of offshore moving fish in the experimental structure (i.e. those entering the rear of the structure) during tests with poppers were consistently lower than their paired controls. Use of the rope net alone did not influence the catch of offshore moving fish. The catches of alewife moving inshore or offshore in the experimental structure when poppers were operating were significantly lower than those during control tests ($p < 0.05$, one-tailed t-tests of log-transformed data). Catches of alewife moving inshore in the experimental frame net during tests of the rope net alone were also significantly lower than during control tests.

Although the catch in the east structure was always greater

TABLE 1. Peak acoustical pressure (kPa) measured at 3 m depth, 1–32 m from the poppers (1, 2, 4, 8, or 12).

Distance (m)	Experimental structure					Control structure				
	1	2	4	8	12[a]	1	2	4	8	12[a]
1	9.9	5.4	5.0	23.9	9	0.4	0.5	0.8	1.4	0.7
2	4.0	3.7	6.9	19.1	7	0.4	0.4	0.6	1.2	0.6
4	2.2	4.1	4.7	10.7	4	0.4	0.5	0.7	1.1	0.6
8	0.9	1.3	2.7	5.7	1.5	0.2	0.5	0.7	1.1	0.8
16	0.8	0.8	1.3	2.6	1.4	0.4	0.4	0.5	1.0	0.5
32	0.4	0.8	0.7	2.3	0.5	0.4	0.7	0.4	1.0	0.6

[a]Measurements from 1983, all others from 1984.

TABLE 2. Mean catches (SD) of alewife moving inshore and offshore in the experimental and east frame nets (*significantly lower than control tests, $p < 0.05$, one-tailed t-tests; **significantly lower than control tests, $p < 0.01$, one-tailed t-tests).

Number of poppers	n	Experimental		East	
		Inshore	Offshore	Inshore	Offshore
1983					
12	7	3.0 (3.2)	2.9 (1.9)	26.4 (15.8)	18.3 (8.5)
12 + RN	8	0.7 (0.8)	4.8 (4.0)	53.7 (38.2)	26.6 (16.1)
0 + RN	6	48.5 (52.4)*	199.2 (207.2)	196.7 (210.2)	137.5 (123.7)
0[b]	11	102.4 (78.9)	117.0 (101.2)	140.5 (85.2)	112.0 (102.2)
1984					
1	8	17.8 (7.4)	15.0 (4.8)	55.6 (20.1)	37.4 (14.7)
2	5	10.4 (7.6)	15.0 (7.4)	38.2 (19.9)	33.0 (9.6)
4	6	15.0 (6.6)	8.2 (6.4)	46.5 (22.5)	24.2 (10.5)
6	4	20.3 (20.6)	3.8 (1.0)	43.3 (39.8)	22.8 (14.8)
8	5	2.4 (3.1)	2.4 (2.9)	8.2 (8.7)	13.2 (15.9)
12	4	12.3 (13.4)	6.3 (5.4)	37.8 (32.6)	31.0 (19.2)
0[b]	10	59.1 (50.6)	64.2 (55.3)	81.2 (65.1)	79.7 (49.3)
All popper tests	47	9.6 (10.6)**	7.6 (6.5)**	41.5 (28.9)**	26.5 (15.0)**
All control tests	21	81.8 (69.0)	91.9 (85.1)	112.2 (99.3)	96.6 (81.1)

[a]RN = rope net.
[b]controls.

than in the experimental structure, the use of poppers on the experimental structure significantly reduced the catch of alewife in the east structure relative to control tests (Table 2). The extent to which the catches in the control structure were reduced was least for one-popper tests. This variation in the extent of influence of poppers on the east structure necessitated the comparison of experimental catches with those of paired control tests in calculating effectiveness indices rather than with concurrent catches in the east structure. Catches in the wing nets were also generally lower during popper tests than during control tests but these differences were not significant ($p > 0.05$, one-tailed t-tests, Table 3). Rope net tests did not influence the catches in the east structure or the wing nets.

In the 1983 tests, the effectiveness in excluding inshore-moving alewife from the experimental structure of the 12-popper array with a rope net and the 12-popper array alone was in excess of 99% (Table 4). In 1984, effectiveness was less, ranging from 71% for one popper to 88% for four poppers. In the 1984 tests, effectiveness did not vary significantly with the number of poppers employed ($p > 0.05$, ANOVA). When the results of 1983 are included in the analysis, significant differences were identified. The effectiveness of combining poppers with a rope net was significantly greater than those for all other tests, except 8 poppers and 12 poppers alone (1983). In addition, that for 12 poppers alone in 1983 was significantly greater than those of 12 poppers alone in 1984 and 1 popper and the rope net alone ($p < 0.05$, Duncan's multiple range test). Similarly, the effectiveness of the poppers in excluding offshore-moving fish ranged from 77% for 1 popper to 96% for 12 poppers alone in 1983. The effectiveness of one popper varied significantly from 12 poppers alone (1983) and the combined poppers and rope net treatment ($p < 0.05$, ANOVA and Duncan's multiple range test).

Sonar Monitoring

Sonar monitoring of the experimental structure revealed relatively low numbers of fish in front of the structure during control and most experimental tests (Fig. 4a). However, during one eight-popper test (Fig. 4b), relatively large numbers of fish moved in toward the structure (not shown) and remained in front of the structure throughout the duration of the test, as indicated by a band of echoes on the sonar output. Although the fish seemed drawn to the experimental structure when the poppers were operating, fish within the band of echoes at the

TABLE 3. Mean catches (SD) of alewife moving inshore and offshore in the wing nets.

Number of poppers	n	Experimental		East	
		Inshore	Offshore	Inshore	Offshore
1983					
12	7	11.7 (10.1)	11.4 (11.6)	8.6 (5.8)	11.4 (5.6)
12 + RN	8	12.9 (17.5)	3.9 (3.7)	17.8 (15.3)	14.0 (11.6)
0 + RN	6	82.2 (102.6)	47.5 (52.9)	50.7 (53.9)	65.3 (77.2)
0[b]	11	44.1 (56.4)	35.1 (49.1)	48.5 (69.0)	45.8 (54.1)
1984					
1	8	28.9 (27.4)	34.3 (14.7)	31.1 (20.9)	40.5 (11.6)
2	5	25.8 (18.6)	34.4 (20.3)	65.0 (46.1)	53.2 (29.7)
4	6	49.2 (22.0)	47.8 (24.5)	80.8 (30.4)	69.0 (30.6)
6	4	34.0 (18.6)	44.5 (32.0)	63.3 (37.0)	61.5 (39.2)
8	5	4.0 (5.8)	7.8 (9.8)	14.4 (16.3)	11.8 (14.5)
12	4	28.3 (29.2)	22.8 (20.2)	30.5 (28.0)	43.3 (22.0)
0[b]	10	39.9 (49.3)	40.4 (49.0)	42.0 (43.0)	55.8 (32.3)
All popper tests	47	23.9 (23.0)	24.6 (22.7)	36.7 (34.5)	35.7 (29.2)
All control tests	21	42.1 (51.9)	35.2 (46.6)	45.4 (56.8)	50.6 (44.2)

[a]RN = rope net.
[b]controls.

TABLE 4. Percent effectiveness (SD) of poppers and rope net in excluding inshore and offshore moving alewife from the experimental structure.

Number of poppers[a]	n	Inshore	Offshore
1983			
12	7	96.1 (2.9)	96.2 (4.5)
12 + RN	8	99.2 (0.8)	95.1 (3.8)
0 + RN	6	73.6 (22.5)	—[b]
1984			
1	8	71.0 (16.1)	77.4 (11.6)
2	5	87.2 (1.6)	83.2 (6.8)
4	6	87.8 (3.4)	85.3 (19.8)
6	4	81.7 (12.6)	90.6 (3.9)
8	5	83.5 (25.0)	87.3 (17.1)
12	4	74.7 (19.8)	83.6 (10.4)

[a]RN = rope net.
[b]Rope net had no influence on offshore moving fish.

structure moved approximately 1−4 m away when the poppers fired. This can be seen in Fig. 4b as small spikes in the band of echoes, the frequency of which approximated the firing rate of the poppers. The species of fish comprising this band of echoes was not determined. Only a few adult alewife were captured in the 3.8-cm-mesh collection nets during the test.

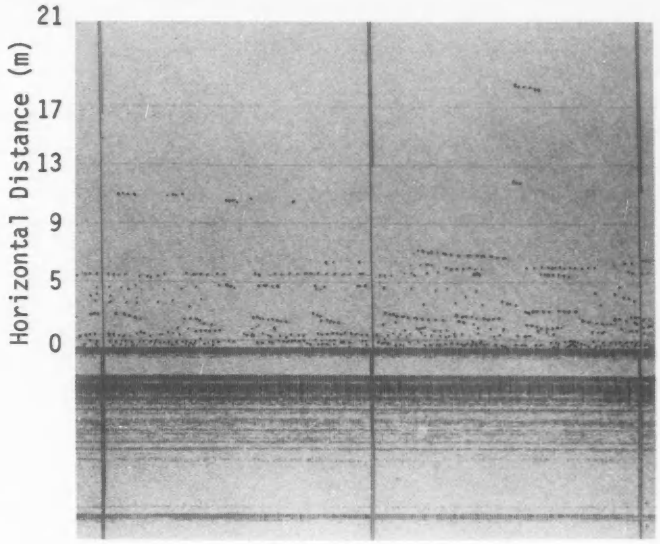
Discussion

Our results clearly demonstrate that low-frequency, high-amplitude sound produced by pneumatic poppers can effectively repel adult alewife. It is not readily apparent why the tests conducted in 1984 failed to achieve the rate of exclusion realized in the 1983 tests; however, lower operating pressures and changes in popper design may have contributed to the observed differences. In the 1984 tests no relationship was found between the number of operating poppers and exclusion effectiveness. However, as a single popper had a lesser effect on the catch of alewife in the east structure compared with that of two or more poppers, the extent of influence of a single popper would appear to be approximately 10 m. The width of the structures was 9 m and they were separated by approximately 10 m.

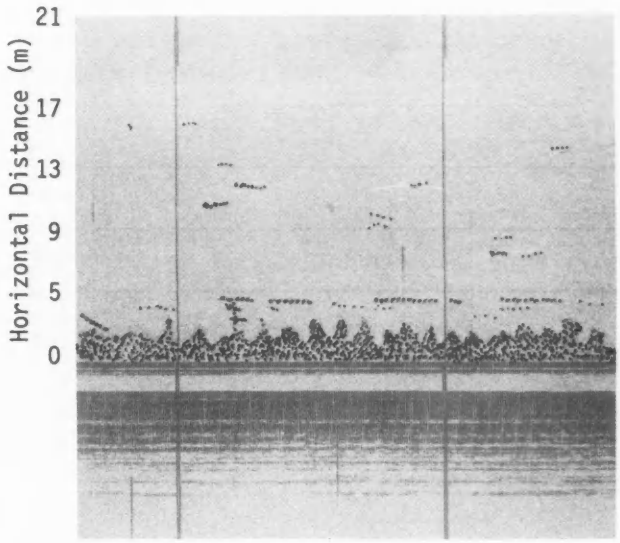
A rope net used in conjunction with the poppers in the 1983 tests did not substantially increase the effectiveness of the popper array. However, as the effectiveness of the poppers alone approached 100%, it is not surprising that the rope net had little additional influence. It is not known whether addition of a rope net in the 1984 tests would have improved the effectiveness of the poppers. In a previous study of the rope net at this facility, an exclusion effectiveness was obtained of approximately 63% during the day and 80% at night (P. H. Patrick and R. W. Sheehan, unpubl. data).

The apparent attraction of fish to the area of the poppers as identified from sonar monitoring of the experimental structure during one test is somewhat inconsistent with the catch results. As the species of fish recorded by the sonar were not identified, one can only speculate on the reasons. Two possible explanations are as follows: first, the fish observed were not adult alewife and were attracted by and passed beyond the poppers but were too small to be captured in the 3.8-cm-mesh gill net; or alternatively, the fish were adult alewife or other species and were attracted to the poppers but held position in front of them and thus were not captured in the nets. As the presence of these bands of echoes were not observed during other monitoring trials during this study or in subsequent tests (P. H. Patrick, unpubl. data), it is our opinion that the fish were not adult alewife but rather small fish which were not catchable in the 3.8-cm mesh and were not normally abundant at the test system during our testing period.

An acoustic stimulus consists of two components, a pressure wave and a particle displacement component associated with the sinusoidal pattern of the sound wave. The acoustico-



(a) Control



(b) Experimental (poppers on)

FIG. 4. Sonar output of fish distribution in front of the experimental structure (a) without poppers operating and (b) with eight poppers operating. Distance from the first set of pilings is indicated.

lateralis system of clupeids is capable of perceiving both of these components (Blaxter and Hoss 1981). Blaxter et al. (1981) found that for Atlantic herring an acoustic signal of a single cycle at 80 Hz and pressures as low as 10 Pa would elicit a directional startle response, and they suggested that although both pressure and particle velocity are involved in determining direction, pressure plays the predominant role in initiating startle responses among clupeids. In this study the peak acoustic pressure measured at 32 m from a single popper was approximately 400 Pa, and was up to 2300 Pa for a multiple popper array. At these pressures a startle response should have been elicited well beyond 32 m from the popper array. Schwarz and Greer (1984) found that at low frequencies, loud sounds that reached highest amplitude rapidly were more effective in eliciting negative responses from Pacific herring than sounds that increased in amplitude gradually. Similarly, Blaxter et al.

(1981) found that a stimulus that required several cycles to reach maximum amplitude was less effective in producing a startle response in Atlantic herring than one that reached maximum amplitude in the first cycle. The pneumatic popper used in our tests met the requirements of low frequency, high amplitude, and rapid rise.

Richard (1968) found that demersal predatory fish species could be attracted by pulsed low-frequency sound (25–50 Hz) and suggested that the low-frequency pulsed sounds mimicked the hydrodynamic disturbances associated with active predation. One would expect that pulsed low-frequency sounds, while attracting predators, would be avoided by prey species such as the alewife. It should be noted that captures of fish other than alewife were rare and four of the eight captures were salmonids which are the major predators of alewife in Lake Ontario. Application of a sound system to exclude fish from intakes may increase entrapment of predators; however, Richard (1968) found that predators rapidly acclimated to the acoustic attractant if the stimulus was not reinforced by prey. Consequently, attraction of predators to the poppers should not last and therefore should not increase their entrapment. As the alewife is a pelagic schooling fish, it is not anticipated that individuals would remain in the influence of the poppers for extended periods of time in an open water situation and acclimation would not likely occur. During this study up to three 2-hr popper tests were conducted in sequence with no reduction in the effectiveness of the poppers over the 6 h of testing.

The reliability of extrapolating these results to other fish species is unclear. In other tests conducted with poppers, yellow perch (*Perca flavescens*) and pumpkinseed sunfish (*Lepomis gibbosus*) were repelled (G. T. Haymes and P. H. Patrick, unpubl. data). However, a device similar to a popper was less effective for nonpelagic species than for pelagic ones (Schuler and Larson 1975). Consequently, use of sound to exclude fish from water intakes, although effective for adult alewife, may not be for all other species. Further studies would therefore be required prior to installation of such a system at a location where alewife is not the primary species of concern.

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Calculating the Sensitivity of a Salmonid Population Model

Geoffrey T. Evans and J. Brian Dempson

Department of Fisheries and Oceans, Fisheries Research Branch, P.O. Box 5667, St. John's, Nfld. A1C 5X1

Evans, G. T., and J. B. Dempson. 1986. Calculating the sensitivity of a salmonid population model. Can. J. Fish. Aquat. Sci. 43: 863–868.

We present a simple model of salmonid life history, and calculate the sensitivity of its outputs to its parameters. Theoretical calculations are preferred to computer simulations. There are some parameters for which the sign of the sensitivity is independent of the actual parameter values. In an uncertain world, management actions aimed at altering such parameters are safer than other actions. For example, habitat protection measures are more certain to have the desired effect than are changes in fishery regulations.

Nous présentons un modèle simple de cycle vital pour les salmonidés et nous calculons la sensibilité des résultats qu'il donne par rapport à ses paramètres. La préférence est accordée aux calculs théoriques plutôt qu'aux simulations sur ordinateur. Il y a certains paramètres pour lesquels le signe de la sensibilité est indépendant de la valeur réelle des paramètres. Dans un monde incertain, les mesures de gestion visant à modifier ces paramètres offrent de meilleures garanties que d'autres mesures. Par exemple, les mesures de protection de l'habitat ont plus de chances d'avoir l'effet désiré que les modifications apportées aux règlements sur les pêches.

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Assessing and predicting the abundance of salmon stocks is an important objective of fisheries management. Publications describing scientific advice (e.g. Dempson 1980; Chadwick 1980; Chadwick and Randall 1983; Randall and Schofield 1983; Gray and Chadwick 1984; Doubleday et al. 1979; Ritter et al. 1980) and research (e.g. Meister 1962; Elson and Tuomi 1975; Gee and Radford 1982; Chadwick 1985) use estimates of parameters governing different parts of the life cycle (e.g. fecundities, mortality rates). There are advantages to considering these parameters in the context of a model of the whole life cycle: for example, consistency places constraints on possible parameter values.

Whether the model is used to reflect understanding or to predict the effects of management actions, it is important to know the sensitivity of its outputs to its parameters. Other things being equal, the parameter to which the model is most sensitive is the most important one to ascertain or consider changing. (Of course, other things might not be equal: this parameter may be difficult to ascertain or change, or may vary greatly.) In this paper we construct a general model of the life history of an anadromous fish like Atlantic salmon (*Salmo salar*) and determine its sensitivity to its various parameters. We emphasize theoretical calculations of sensitivity in preference to computer simulations for particular parameter values.

The Model

The model comprises a list of the life history stages of a salmon (1+ parr, smolt, spawning female grilse, etc.) together with the fractions moving from one stage to another (Fig. 1). The parameters P_i are survival fractions: a fraction P_i of a stage survives to the next stage. (Fecundities can be thought of as fractions greater than 1.) Parameters Q_i are splitting fractions: a stage splits between two subsequent stages in fractions Q_i and $(1 - Q_i)$. Density-dependent (nonlinear, feedback) terms enter in only one place. Tracing the paths from hatched egg to eggs laid involves constant fractions so that if x eggs hatch, Bx eggs will be laid in the next generation where B is a number that depends on the parameters but not on x. The last step, from eggs laid to eggs hatched, is density dependent: if Bx are laid then $\phi(Bx)$ will hatch, where ϕ is some function more complicated than a simple multiple. In general, as the number of eggs increases, the fraction that will hatch decreases, because of spawning in marginal habitat or disturbing previously laid eggs, for example. The total number hatching might increase or decrease.

Although this model, with only one form of density dependence, is very simple, it is structured so that more complicated relations can be built in as they become known.

Analysis of the Model

Definition of Sensitivity

Let us assume that the model does describe some salmon river, and that the parameter values have been unchanged long enough that the river, and the model that represents it, have come to equilibrium. We can combine all possible pathways from hatching to egg laying: even though different pathways can take between 3 and 6 yr, the years in which they produce eggs will all be identical. (It is not mathematically necessary that the model have a positive equilibrium, let alone a stable one; the stream we are considering is slightly, although not unreasonably, special.) Sensitivity analysis can address at least three questions. (1) If one of the parameters is changed, how much do equilibrium abundances and catches change? There could be either a real change in the parameter because of management actions, or a change in our best estimate of it. (2) If a parameter changes, what are the immediate, transient changes as the system moves from its previous equilibrium to its new one? (3) If our estimate of a parameter changes, and we

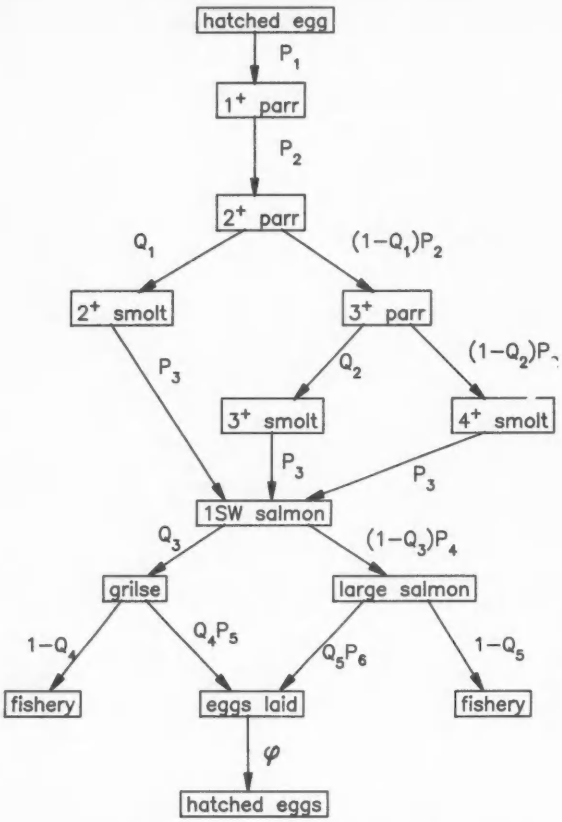

FIG. 1. Structure of the salmon model. The interpretation of the parameters is as follows: P_1: first-year survival; fraction of hatching eggs that become 1+ parr; P_2: survival fraction for each subsequent river year; Q_1: fraction of 2+ parr that become 2+ smolts; Q_2: fraction of 3+ parr that become 3+ smolts (without mortality, the smolt age composition would be Q_1: $(1 - Q_1)$ Q_2: $(1 - Q_1)(1 - Q_2)$ $2's$: $3's$: $4's$); P_3: survival fraction in the first year at sea; Q_3: fraction of one sea winter (1 SW) fish that return as grilse; P_4: survival fraction in the second year at sea; Q_4: fraction of grilse surviving the fishery; P_5: number of eggs per grilse; the production of proportion of females in the grilse and the fecundity of female grilse; Q_5: fraction of large salmon surviving the fishery; P_6: number of eggs per large salmon.

trust our estimates of equilibrium abundances, how much must other parameters change to retain a consistent model? We shall address only the first two questions.

We want to know how a particular output X, like total spawning stock or catch of large salmon, reacts to change in particular parameter P (dropping the subscripts for ease of writing; there is no difference here between a survival fraction and a splitting fraction). We shall use a measure of relative sensitivity: if there is a change ΔP in P, then the relative change in P is $\Delta P/P$. If this produces a relative change $\Delta X/X$ in X, then the relative sensitivity is

$$\frac{\Delta X/X}{\Delta P/P} = \frac{P}{X}\cdot\frac{\Delta X}{\Delta P}$$

or, taking the infinitesimal limit,

$$(1)\quad \epsilon(X,P) = \frac{P}{X}\cdot\frac{\partial X}{\partial P} = \frac{P}{X}X_P$$

(using the subscript to denote partial differentiation).

This is a convenient choice for two reasons. First, it is a dimensionless number, so we get the same answer for ϵ whether we measure salmon in numbers or kilograms. Second, if an output X is just a multiple of one parameter (whatever its relation to other parameters):

$$X = P_1\cdot f(P_2, P_3, \ldots)$$

then

$$X_{P_1} = f(P_2, P_3, \ldots)$$

and

$$\frac{P_1}{X}X_{P_1} = \frac{P_1}{P_1\cdot f(\ldots)}\cdot f(\ldots) = 1.$$

This is intuitively clear: a 5% (say) change in P_1 in this model will produce a 5% change in X. In the salmon model, the outputs are largely but not entirely determined by products of the parameters. Therefore the deviation of the ϵ's from 1 gives an idea of how the model differs from a multiplicative model.

In economics, the quantity ϵ is known as the elasticity of the function (e.g. Chiang 1967, p. 198). Caswell et al. (1984) calculated elasticities for a similar salmon model, although they required an equilibrium only for the age structure and not for the total numbers in the population.

Existence and Stability Requirements

Recall that if x eggs hatch, then Bx eggs are laid, and $\phi(Bx)$ of them hatch. To have an equilibrium, the number of eggs hatching from Bx eggs laid must be precisely the number of hatched eggs needed to produce Bx eggs laid:

$$\phi(Bx) = x.$$

The equilibrium number of eggs hatching is a solution to this equation; we are interested only in models for which the equation has a positive solution.

Moreover, the equilibrium should be stable: small perturbations of x from its equilibrium value should become smaller in subsequent generations. If ξ is the equilibrium number: $\phi(B\xi) = \xi$, and $x > \xi$, then for stability fewer eggs must hatch in the next generation: $\phi(Bx) < x$. Similarly, if $x < \xi$, then we must have $\phi(Bx) > x$. So, near ξ the slope of $\phi(Bx)$ must be less than the slope of x, which is 1: $\phi_x(Bx) < 1$, as in Fig. 2.

On the other hand, the slope of ϕ cannot be too strongly negative, or we might have growing oscillations: $x > \xi$, $x_1 = \phi(Bx) < \xi$, and $x_2 = \phi(Bx_1) > x > \xi$. Thus, for a locally stable equilibrium we must have

$$-1 < \phi_x(Bx) < 1.$$

Levin and Goodyear (1980) discussed the oscillations possible in age-structured populations if $\phi_x(Bx) < -1$.

Sensitivity Analysis: General

The outputs, numbers of fish in different stages, are all of the form $X = xy$ where x is the number of eggs hatching and y is some function of the parameters that determines the specific output as a function of the number of eggs hatching. For example, if X is the number of fish that survive the first sea winter, then

$$y = P_1P_2[Q_1 + (1 - Q_1)P_2(Q_2 + (1 - Q_2)P_2)]P_3.$$

The elasticity of a product is the sum of the elasticities

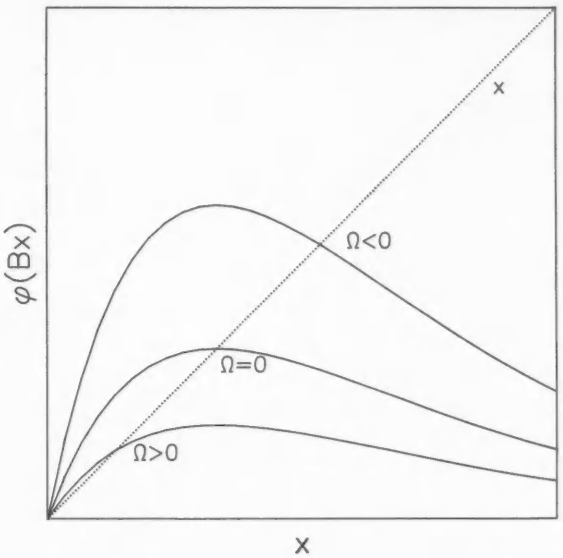

FIG. 2. "Acuteness" parameter Ω for different shapes of ϕ.

(Nievergelt 1983), so

$$\epsilon(X,P) = \epsilon(y,P) + \epsilon(x,P).$$

To determine x_P, we differentiate the equilibrium equation $\phi(Bx) = x$:

$$\frac{\partial}{\partial P}\phi(Bx) = [x\cdot B_P + B\cdot x_P]\cdot\phi'(Bx) = x_P$$

(where the prime denotes differentiation of ϕ with respect to its total argument Bx). Collecting the terms in x_P:

$$x_P = \frac{\phi'(Bx)}{1 - B\phi'(Bx)}\,x\cdot B_P$$

$$\frac{P}{x}x_P = \frac{B\phi'(Bx)}{1 - B\phi'(Bx)}\frac{P}{B}B_P$$

or

$$\epsilon(x,P) = \Omega\cdot\epsilon(B,P)$$

where

$$(2)\quad \Omega = \frac{B\phi'(Bx)}{1 - B\phi'(Bx)} = \frac{\phi_x(Bx)}{1 - \phi_x(Bx)}.$$

Roughly speaking, Ω measures the acuteness of the intersection of $\phi(Bx)$ with the 45° replacement line (Fig. 2). More precisely, it is the sensitivity of that intersection point to a leftward displacement of ϕ. Because $-1 < \phi_x(Bx) < 1$, we have $-\frac{1}{2} < \Omega < \infty$.

To summarize, the relative sensitivity of X to P, where $X = xy$, is

$$(3)\quad \epsilon(X,P) = \epsilon(y,P) + \Omega\cdot\epsilon(B,P).$$

This has three parts: the relative sensitivity of y to P, where y determines the specific output X given the number of eggs hatched; the relative sensitivity of B to P, where B determines the eggs laid per egg hatched and is independent of the choice of X; and the number Ω, independent of the choice of X and P, which contains all the effects of density dependence and the requirement of equilibrium. Determining one ϵ gives much of the information needed to calculate all of them.

Another way to look at the splitting of the sensitivity formula is short-term, direct effects plus long-term, feedback effects. $\epsilon(y,P)$ describes the effect that occurs within a generation: increasing fishing effort at first increases yield. $\Omega\cdot\epsilon(B,P)$ describes the long-term effects, on equilibrium numbers, of the feedback loop involving ϕ.

Sensitivity Analysis: Specific

For the salmon model we are considering

$$B = P_1P_2[Q_1 + (1 - Q_1)P_2(Q_2 + (1 - Q_2)P_2)] \times P_3[Q_3Q_4P_5 + (1 - Q_3)P_4Q_5P_6].$$

Let us consider, as an example, sensitivities of the catch of grilse. For this output,

$$y = P_1P_2[Q_1 + (1 - Q_1)P_2(Q_2 + (1 - Q_2)P_2)] \times P_3Q_3(1 - Q_4).$$

We now compute the relative sensitivity to various parameters.

P_1: *survival from hatching to 1+ parr*

Here we use the rule for multiples: y and B are both of the form $P_1\cdot f(\ldots)$ where f is a function not involving P_1; so,

$$\epsilon(y,P_1) = \epsilon(B,P_1) = \epsilon_1 = 1$$

and therefore

$$\epsilon(X,P_1) = 1 + \Omega = \frac{1}{1 - B\phi'(Bx)} > 0.$$

P_3, survival over the first sea winter, works the same way.

P_2: *survival in subsequent river years*

The rule about simple multiples generalizes: if

$$X = f(P_2)\cdot g(\ldots)$$

where g is a function not involving P_2, then

$$X_{P_2} = f'(P_2)\cdot g(\ldots)$$

and

$$\epsilon(X,P_2) = P_2\cdot f'(P_2)/f(P_2)$$

regardless of the other parameters. Therefore we need consider only the part

$$P_2[Q_1 + (1 - Q_1)P_2(Q_2 + (1 - Q_2)P_2)]$$

of y and B:

$$\epsilon(y,P_2) = \epsilon(B,P_2) = \epsilon_2$$

$$= \frac{Q_1 + 2(1 - Q_1)Q_2\cdot P_2 + 3(1 - Q_1)(1 - Q_2)\cdot P_2^2}{Q_1 + (1 - Q_1)Q_2\cdot P_2 + (1 - Q_1)(1 - Q_2)P_2^2} > 1$$

and

$$\epsilon(X,P_2) = (1 + \Omega)\cdot\epsilon_2.$$

$\epsilon_2 > 1$ because of the squared and cubed terms involving P_2.

Q_1: *fraction of 2+ parr that becomes smolts*

As with P_2, we have

$$\epsilon(y,Q_1) = \epsilon(B,Q_1) = \epsilon_\alpha$$

$$= 1 - \frac{P_2(Q_2 + (1 - Q_2)P_2)}{Q_1 + (1 - Q_1)P_2(Q_2 + (1 - Q_2)P_2)}$$

so

$$\epsilon(X, Q_1) = (1 + \Omega)\cdot\epsilon_\alpha \text{ where } 0 < \epsilon_\alpha < 1.$$

ϵ_α is less than 1 because smolting at a later age, although it reduces the chance of survival, does not eliminate it. If $P_2 \approx 0$, so that smolting at age 2 is almost essential to survival, then $\epsilon_\alpha \approx 1$ (recall $\epsilon_1 = 1$); if $P_2 = 1$, so that smolting age is irrelevant to survival, $\epsilon_\alpha = 0$. The sensitivity to Q_2 is computed similarly.

Q_3: *the fraction of one sea winter (1SW) fish that become grilse*

$$\epsilon(y, Q_3) = 1.$$

$$\epsilon(B, Q_3) = \frac{Q_3Q_4P_5 - Q_3P_4Q_5P_6}{Q_3Q_4P_5 + (1 - Q_3)P_3Q_5P_6}.$$

If we define

$$E_g = \frac{Q_3Q_4P_5}{Q_3Q_4P_5 + (1 - Q_3)P_4Q_5P_6}$$

= fraction of eggs laid by grilse

$$E_a = \frac{(1 - Q_3)P_4Q_5P_6}{Q_3Q_4P_5 + (1 - Q_3)P_4Q_5P_6}$$

= fraction of eggs laid by large salmon

so that $E_g + E_a = 1$, then

$$\epsilon(B, Q_3) = \frac{E_g - Q_3\cdot E_a}{1 - Q_3} = \frac{E_g - Q_3}{1 - Q_3} < 1.$$

Then

$$\epsilon(X, Q_3) = 1 + \Omega\frac{E_g - Q_3}{1 - Q_3}.$$

Whereas all the ϵ's calculated previously have been positive, and we have known whether they were greater than or less than $(1 + \Omega)$, things are now less certain. It is possible that $E_g < Q_3$ (since grilse are less fecund than large salmon), in which case if Ω is large ($\phi_x(Bx) \approx 1$; the equilibrium is close to instability), then $\epsilon(x, Q_3)$ is negative. We can no longer know even the sign of ϵ without knowing more details about the model and its parameter values.

Parameters of the egg hatch function

Next consider sensitivities to the parameters of ϕ, the density-dependent function determining egg hatch. For any parameter R, $\partial y/\partial R = 0$, and therefore $\epsilon(X, R) = \epsilon(x, R)$. Consider for example the Ricker function

$$\phi(Bx) = ABx \exp(-Bx/R).$$

At equilibrium, $\phi(Bx) = x$, so $x = \ln(AB)\ R/B$ and $\epsilon(x, R) = 1$. Therefore the relative sensitivity of any output X to the Ricker parameter R is 1 (and therefore a relative sensitivity of 1 does not always mean the parameter enters as a multiple.) Also $\epsilon(x, A) = 1/\ln(AB)$. Notice that $\Omega = (1 - \ln(AB))/\ln(AB)$, $1 + \Omega = 1/\ln(AB)$, so that $\epsilon(X, P_1) = 1 + \Omega = \epsilon(X, A)$, as expected because P_1 and A behave identically in the model.

Sensitivities to other parameters can be worked out as desired. Notice that P_5, the number of eggs per grilse, is the product of two numbers: the fraction of grilse that are female and the fecundity of a female grilse. It is easy to show that the sensitivity to P_5 is the same as the sensitivity to either of its factors.

Numerical Simulations

Analytic techniques for calculating sensitivity make it easy to identify potentially interesting areas of parameter space, but they become tedious once the interesting ideas have been found. At this stage, it is reasonable to turn to computer simulation. A particular instance of the model was run with the parameters $P_2 = 0.54$, $Q_1 = 0.2593$, $Q_2 = 0.94$, $Q_3 = 0.5$, $Q_4 = 0.45$, $Q_5 = 0.15$, and other parameters such that $E_g = 0.28$, $E_a = 0.72$, and $B = 3.25$. The estimate of parr survival comes from Chadwick (1982a); the lower estimates of Evans et al. (1984) and Myers (1984) did not support a positive equilibrium when combined with the other parameters. The maturation fractions come from Murray (1968) and the fishing escapements from Anonymous (1978). We used the Ricker function $\phi(Bx) = 0.37Bx \exp(-Bx/2\cdot10^6)$ so that $x = 112720$ and $\Omega = 4.47$. The low-density egg survival fraction 0.37 was taken from Chadwick (1982b); the quotient of $2\cdot10^6$ eggs is an arbitrary normalization to a particular size of stream. The resulting simulated population has a survival from egg to smolt (mean age 2.6 yr) of 2.4% and from smolts to escaping adults of 4%, with 17% of the escapement made up of large salmon. Large salmon constitute 48% of the catch by number, or 72% by weight. The sensitivity of the grilse catch to selected parameters is

$$P_1\text{: } 5.47;\ P_2\text{: } 8.86;\ Q_1\text{: } 1.04;\ Q_3\text{: } -0.98.$$

By running simulations with slightly perturbed parameter values until the model comes to equilibrium, we have confirmed these numbers, and computed others (Table 1). There is a set of parameters $(P_1, P_2, P_3, P_5, P_6, Q_1, Q_2)$ which influence all outputs equally. Notice that, because of the much greater fecundity of large salmon, if the fraction of salmon that returns as grilse increases, the equilibrium population of grilse decreases. This is because the indirect effects of maturing as a large salmon and laying more eggs, some of which mature as grilse, outweigh the direct effects of maturing as a grilse. (Grilse and large salmon are not assumed to breed true.)

Management Implications

Two parameters whose values are somewhat under human control are the spawning escapement fractions of grilse (Q_4) and large salmon (Q_5):

$$\epsilon(B, Q_4) = E_g;\ \epsilon(B, Q_5) = E_a$$

$$\epsilon(y, Q_4) = -Q_4/(1 - Q_4);\ \epsilon(y, Q_5) = 0.$$

z, the function for large salmon catch corresponding to y, is proportional to $1 - Q_5$ and independent of Q_4, so

$$\epsilon(z, Q_4) = 0;\ \epsilon(z, Q_5) = -Q_5/(1 - Q_5).$$

Let G denote the catch of grilse and A the catch of large salmon. Then

$$\epsilon(G, Q_4) = -Q_4/(1 - Q_4) + \Omega\cdot E_g$$

$$\epsilon(A, Q_4) = \Omega\cdot E_g$$

$$\epsilon(G, Q_5)\ \Omega\cdot E_a$$

$$\epsilon(A, Q_5) = -Q_5/(1 - Q_5) + \Omega\cdot E_a.$$

TABLE 1. Sensitivity of selected outputs to the parameters (the sensitivity to P_3 is the same as to P_1).

	Survival fractions P					Splitting fractions Q				
	1	2	4	5	6	1	2	3	4	5
Escapement										
Large salmon	5.47	8.86	4.22	1.24	3.22	1.04	1.46	−2.98	1.24	4.22
Grilse	5.47	8.86	3.22	1.24	3.22	1.04	1.46	−0.98	2.55	3.22
Total	5.47	8.86	3.39	1.24	3.22	1.04	1.46	−1.31	2.08	3.39
Harvest										
Large salmon	5.47	8.86	4.22	1.24	3.22	1.04	1.46	−2.98	1.24	3.04
Grilse	5.47	8.86	3.22	1.24	3.22	1.04	1.46	−0.98	0.43	3.22

Consider the effect of changing Q_4 and Q_5 in the same proportion:

$$\begin{aligned}\epsilon(G, Q_4 \text{ and } Q_5) &= \epsilon(G, Q_4) + \epsilon(G, Q_5)\\ &= -Q_4/(1 - Q_4) + \Omega\\ &= \frac{-Q_4}{1 - Q_4} + \frac{\phi_x(Bx)}{1 - \phi_x(Bx)}\\ &= \frac{\phi_x(Bx) - Q_4}{(1 - Q_4)(1 - \phi_x(Bx))}\\ &> 0 \text{ if and only if } \phi_x(Bx) > Q_4.\end{aligned}$$

An increase in total escapement produces an increase in grilse catch if $\phi(Bx)$ is an increasing function of x, with a slope $>Q_4$. Because $0 < Q_4 < 1$ and $-1 < \phi_x(Bx) < 1$ (by the stability requirement), if $Q_4 \approx 1$, it is unlikely that $\phi_x(Bx)$ will be $>Q_4$. In other words, if almost all the grilse escape to spawn (and therefore almost none are caught), increasing escapement will probably decrease yield. Notice also that if $Q_4 \approx 1$, then $1 - Q_4 \approx 0$, and because this term appears in the denominator of the expression for ϵ, ϵ will be very large. This is an artificial sort of result: if almost all the grilse escape, then a small relative change in the number that escape means a large relative change in the number that are caught. An increase in escapement from 98 to 99% means a 50% reduction in percentage caught.

If $Q_4 \approx 0$ (almost all the grilse are caught), then the sign of ϵ depends on the sign of $\phi_x(Bx)$. If it is positive (more eggs laid means more hatch), then increasing escapement will increase yield; if it is negative, then increasing escapement will decrease yield.

Notice the contrast between two sets of parameters: $\{P_1, P_2, Q_1, Q_2, P_3\}$ and $\{Q_3, Q_4, P_4, P_5, Q_5, P_6\}$. The first set influences the specific output function y and the egg-laying function B in the same way, and therefore the relative sensitivity to any of them is proportional to $1 + \Omega$ and is known to be positive. This means that even if increasing P_2, say, decreases the equilibrium number of eggs hatching, it still increases yield: the feedback effects that may lead to a smaller hatch are outweighed by the direct effects of increased post-hatch survival. Contrast this with the parameters in the second set, for which we cannot be sure of the sign of the sensitivity without knowing much more about the model parameters. Therefore, measures that change parameters in the first set (habitat protection measures, for example) are intrinsically safer than measures that change parameters in the second set (changes in fishery regulations, for example): even if the system was not fully understood, the equilibrium yield will move in the intended direction.

Discussion

The analytical approach allows results to be derived in greater generality, and points out when it is worth searching further in parameter space — where surprises might lie. A less obvious benefit is that mistakes are often easy to identify because they fail to conform to certain general patterns. Computer simulation, on the other hand, will work on models that are too complicated to analyse. As more complicated functional relationships between life history stages are identified, they can be incorporated into the simulation much more easily than into the analysis. A tandem approach works best.

We have discussed only local, infinitesimal sensitivity and not the consequences of large changes in parameter values. For specific changes, the best approach is simply to calculate the new equilibrium (either by algebra or by simulation). For a more systematic study, one can still be confident of the signs for the group $\{P_1, P_2, Q_1, Q_2, P_3\}$: any large change is the sum of many small changes, and the relative sensitivity is known to be positive for each small change. Thus the comments about the safety of habitat protection measures apply equally to large changes.

Many parameters enter y and B in the same way, so that the sensitivity ϵ is a multiple of the "acuteness" parameter $(1 + \Omega)$. It is worth commenting on the role of $(1 + \Omega)$. If $\Omega > 0$ (i.e. $\phi'(Bx) > 0$: the more eggs that are laid, the more will hatch), then $(1 + \Omega)$ amplifies sensitivity. If $\Omega < 0 <$ the more eggs that are laid, the fewer will hatch), then $(1 + \Omega)$ reduces sensitivity. If $\Omega = 0$ (corresponding to the maximum number of eggs hatching), then $\epsilon(X, P) = \epsilon(y, P)$. This makes sense: when the derivative is zero, the number of eggs hatching is not sensitive to changes in the parameters. The high sensitivity when $\Omega > 0$ can be interpreted in another way. The curves of x and $\phi(Bx)$ are nearly parallel; only a small amount of density dependence is needed to produce an equilibrium; the stream is on the verge of not being able to support a population at all (see Fig. 2). Clearly if two curves are nearly parallel, their intersection point is very sensitive to small changes in one of the curves. In these circumstances also, the rate of return to equilibrium is slow and the equilibrium solution may have less practical importance. The method is best suited to streams with firmly established populations, for which sensitivities will be relatively small and return times relatively fast.

The most serious inaccuracy of the model is probably the assumption that density dependence enters only at one stage. There are density effects in the parr as well (Symons 1979; Buck and Hay 1984): high parr densities may increase the age at smolting and therefore decrease fry-to-smolt survival. If such effects are important, then our conclusions about the auto-

matic safety of habitat protection measures are less secure. Also, if the equilibrium lies on a steeply descending part of a Ricker (or similar) curve, then there is a possibility of inducing oscillatory instability, whereupon predicting the change in equilibrium will be less important. Still, the general conclusion remains that habitat protection measures are more likely to have the desired effect than are changes in fishery regulations.

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Interaction of Low pH and Starvation on Body Weight and Composition of Young-of-Year Smallmouth Bass (*Micropterus dolomieui*)[1]

G. L. Cunningham

Department of Zoology, University of Toronto, Toronto, Ont. M5S 1A1

and B. J. Shuter

Ontario Ministry of Natural Resources, Research Section, Fisheries Branch, Box 50, Maple, Ont. L0J 1E0

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Effects of overwinter starvation on the body composition of young-of-year smallmouth bass (*Micropterus dolomieui*) were examined in laboratory and field studies. Interactive effects of starvation and low pH on body composition were examined in the laboratory. Changes in body composition associated with starvation were similar in laboratory and field studies: on a dry weight basis, the amount of water, ash, Ca, K, and Na increased progressively in both laboratory and wild fish. The amount of Cl per unit dry weight showed a moderate increase in the laboratory fish and a large decline in the wild fish. The effects on starving fish of 6-wk chronic exposures to nonlethal pH levels of 4.0–7.0 were examined in the laboratory. No pH effect was noted for levels greater than 5.0. Losses of water, ash, Ca, K, Cl, and Na increased as the pH declined. There was no consistent effect of pH on rate of loss of ash-free organic matter. The results suggest that starvation may reduce the tolerance of young smallmouth bass to low pH through progressive weakening of the osmoregulatory system.

Les effets du manque de nourriture en hiver sur la composition chimique du corps de l'achigan à petite bouche (*Micropterus dolomieui*) dans sa première année ont été examinés en laboratoire et sur le terrain. Les effets interactifs du manque de nourriture et d'un faible pH sur la composition chimique ont été examinés en laboratoire. Les changements dans la composition chimique associés au manque de nourriture étaient semblables au laboratoire et sur le terrain : en masse sèche, les quantités d'eau, de cendre, de Ca, de K et de Na augmentaient progressivement dans le poisson tant en laboratoire qu'en liberté. La quantité de Cl par unité de masse sèche présentait une augmentation modérée dans le poisson en laboratoire et une forte diminution dans le poisson en liberté. On a examiné aussi en laboratoire les effets, sur le poisson privé de nourriture, d'une exposition constante de 6 sem à des niveaux non létaux de pH de 4,0 à 7,0. Aucun effet dû au pH n'a été noté pour des valeurs supérieures à 5,0. Les pertes d'eau, de cendre, de Ca, de K, de Cl et de Na ont augmenté au fur et à mesure que le pH diminuait. Le pH n'a pas eu d'effet uniforme sur l'importance des pertes de matière organique sans cendre. Les résultats indiquent que le manque de nourriture peut réduire la tolérance du jeune achigan à petite bouche aux faibles pH par affaiblissement progressif du système osmorégulatoire.

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The smallmouth bass (*Micropterus dolomieui*) is a warmwater sports fish of economic importance to the recreation and tourism industry of Ontario. Data on the disappearance of wild populations indicate that the species is sensitive to acidification through recruitment failure (Harvey 1980). Baynes (1981) and Beamish (1976) suggested that reproductive failure becomes likely when pH falls within the range from 5.5 to 6.0. However, the phases of the life cycle vulnerable to reduced pH have yet to be identified.

Shuter et al. (1980) argued that much of the considerable year-to-year variation in cohort strength, which is characteristic of northern populations of this species, can be accounted for by variations in the winter survival of young-of-year. Feeding at winter temperatures is significantly reduced, and metabolic requirements must be largely supplied by energy reserves accumulated during the first growing season. Under annual temperature cycles typical of north-central Ontario (i.e. at the northern limit of the species' range), the first growing season is sufficiently short and the winter sufficiently long that significant mortality from starvation is likely. For such populations, an increase in metabolic costs arising from exposure to reduced pH levels could lead to a significant decrease in the winter survival of young-of-year and, consequently, a greater likelihood of recruitment failure.

In this study, we examine the effects of low pH on the metabolic costs of young-of-year smallmouth bass held under simulated winter conditions, and we document the interactive effects of starvation and low pH on whole-body elemental composition. We also compare changes in body composition observed under laboratory conditions with changes observed in three wild populations over the winter of 1981–82.

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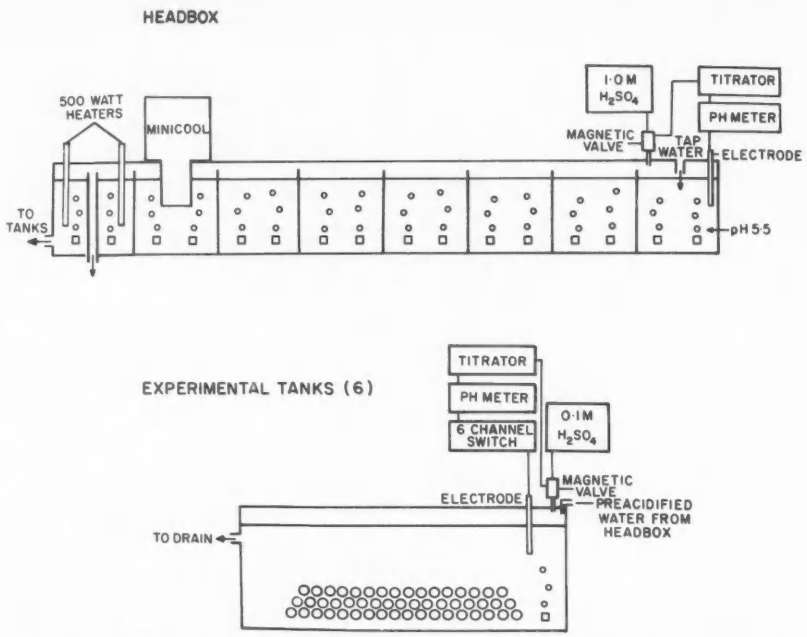

FIG. 1. pH control system. Water from the headbox is fed to six experimental tanks, each maintained at a different pH.

TABLE 1. Summary of conditions for three experiments successfully completed. In each experiment, the six pH levels tested were checked at least once every 2 d; for 97% of these checks, the observed pH was within 0.2 unit of the desired level. Temperatures were checked daily and were within 1°C of the reported mean for 96% of these checks.

Experiment	Source of fish	Duration	pH levels tested	Mean fork length (cm)	Fork length range (cm)	Mean temperature (°C)
1	OMNR hatchery	Dec. 12, 1981 – Jan. 26, 1982	3.5, 4.2, 4.9, 5.6, 6.3, 7.0	6.25	4.9–7.6	5.86
2	Northeastern Biologists	Sept. 15, 1982 – Oct. 26, 1982	4.0, 4.3, 4.6, 4.9, 5.6, 6.5	6.7	5.3–9.6	7.81
3	Northeastern Biologists	Nov. 1, 1982 – Dec. 12, 1982	4.0, 4.3, 4.6, 4.9, 5.6, 6.5	6.4	5.3–9.0	6.05

Materials and Methods

Young-of-year smallmouth bass for laboratory experiments were obtained from the Ontario Ministry of Natural Resources (OMNR) hatchery on Manitoulin Island in 1981 and from Northeastern Biologists in Rhinebeck, New York, in 1982. In the late summer of each year, approximately 1300 fish were transferred to a large (3000 L) flow-through holding tank at the University of Toronto. Initially, photoperiod, and temperature conditions in the holding tank were set to match conditions experienced by the fish in the hatchery. Day length and temperature were then decreased gradually to simulate an accelerated change to winter conditions. On reaching 10.25 h light: 13.75 h dark and 6°C, no further adjustments were made to photoperiod or temperature. The holding and test tanks were maintained under these conditions throughout the experiments. Temperature was maintained using Minicool refrigeration units and thermoregulator-controlled glass rod heaters. Opaque fiberglass covers were placed over both the holding and test tanks to minimize the amount of light reaching the fish, thus simulating the effects of ice and snow cover. In both holding and test tanks, one piece of PVC tubing (2.5 cm diameter, 12 cm long) was provided for each fish to simulate the rocky shelters used by wild young-of-year during the winter.

Four experiments were started: two in the winter of 1981–82 and two more in the fall of 1982. Of these, only three were completed successfully (Table 1). Each experiment lasted six weeks. In each experiment, six test tanks were maintained at different pH levels, 1 tank for each pH level (Table 1). Because the available water (dechlorinated tap water) was quite hard (120–140 mg $CaCO_3 \cdot L^{-1}$ similar to levels observed at both hatcheries), direct acidification would liberate potentially toxic amounts of CO_2. Thus, the water was pretreated before reaching the test tanks by mixing it with 1 *M* H_2SO_4 in the first section of a headbox divided into eight sections by perforated Plexiglas partitions (Fig. 1). The pH in the first section was maintained at 5.5 by a Radiometer PHM84 pH meter and TTT80 titrator, in conjunction with a GK2401C combination electrode and an MNV2 magnetic valve. Each section in the headbox was vigorously aerated to drive off evolved CO_2. As

a consequence of CO_2 loss, the pH in the final section fluctuated from 6.5 to 7.0.

Water flowed by gravity from the last section of the headbox to the six 90-L test tanks. The flow rate to each tank was maintained at approximately 0.075 $L \cdot min^{-1}$. A six-channel switch (Bach-Simpson SAS-2) was used to permit a single pH meter (PHM84) and titrator (TTT80) to control the pH in all six test tanks. The switch caused the pH meter and titrator to successively monitor (via a GK2401C electrode) and adjust (using 0.1 *M* H_2SO_4 delivered via an MNV2 magnetic valve) the pH of each tank for 2 min out of every 10. Each tank was well aerated to insure adequate mixing of the acid, acceptable O_2 levels (12−13 $mg \cdot L^{-1}$), and to drive off any further CO_2 produced by acidification.

At the start of each 6-wk experiment, 300 fish were taken from the holding tank and equally distributed among the six test tanks. An additional 50 fish were then taken from the holding tank and killed. This latter sample was used to obtain data on the body composition of the fish at the start of each experiment. Each test tank was maintained at a different pH for a period of 6 wk. Temperatures were checked and adjusted on a daily basis. A complete pH check, and calibration of the pH control system, was carried out at least every second day. Tanks were checked twice daily for dead fish. Periodically, the water in the headbox and test tanks was analyzed for metal (Al, Cu, Fe, Mn, Ni, Zn) levels. These were always well below the minimum toxic levels reported by Spry et al. (1981). At the end of 6 wk, all fish in the test tanks were killed.

Fish that lived through an experiment, those that died during an experiment, and those sacrificed from the holding tank at the beginning of an experiment were all processed in the same manner. Live fish were killed with an overdose of MS-222. Fish were blotted dry, weighed to the nearest milligram, measured (fork and total length to the nearest millimetre), wrapped in aluminum foil, and frozen. Frozen fish were reweighed and measured, oven dried at 110 ± 5°C for 24 h, placed in a desiccator for 8 h, and then re-weighed to determine dry weight. Dried fish were placed in a muffle furnace at 550 ± 10°C for 24 h. Remaining ash was placed in a desiccator for 8 h and then weighed a final time. Elemental composition (levels of Na, K, Cl, Ca in micrograms per gram) of the whole-body ash was determined by neutron activation analysis using a Slowpoke-2 nuclear reactor. Samples were irradiated at a neutron flux of 2×10^6 neutrons $\cdot cm^{-2} \cdot s^{-1}$ for 1 min. After a 1-min delay, the radioactivity of each sample was determined using a gamma ray spectrophotometer. The concentration (micrograms per gram) of each element in the sample was determined by comparing its activity with the activity of a standard of known concentration. Data on elemental composition of fish are available for part of experiment 1 and all of experiments 3 and 4.

The fish held at pH 3.5 in experiment 1 all died within 2 wk of the start of the experiment. The pH 3.5 fish in experiment 2 all died within 2 d of the start. In experiment 2, a fungus infection broke out in five of the test tanks part way through the experiment, and many fish died before the end of the 6 wk. Therefore, the data from pH 3.5 in experiment 1 and all of the data from experiment 2 were excluded from further analysis.

The effects of starvation on the test animals were evaluated by comparing the following measures of body composition in the samples taken from the holding tank at the beginning of each experiment with similar measures taken on fish in the highest pH tank at the end of 6 wk: wet weight, ash weight, ash-free dry weight (i.e. dry weight minus ash weight), and the Na, K, Cl, and Ca concentrations. The interactive effects of starvation and reduced pH were evaluated by comparing the same measures of body composition across the samples collected from the six test tanks at the end of each 6-wk experiment. Comparisons of wet weight, ash weight, and ash-free dry weight across samples were done using analysis of covariance on log-transformed data with log fork length as the covariate. Results are presented in the form of estimates of mean weight at a standardized fork length of 6.4 cm. Comparisons of Na, K, Cl, and Ca across samples were done using one-way analysis of variance on untransformed data. Length was not used as a covariate here, because it was not significantly correlated with any of the elemental values. The statistical significance of each comparison was evaluated using a two-tailed *t*-test. Tests on independent replicates of the same comparison were pooled using a χ^2 procedure (Sokal and Rohlf 1981, p. 779) to obtain an overall test of significance.

Samples of young-of-year smallmouth bass were obtained from wild populations resident in three small lakes located in south-central Ontario (Table 2). Samples were collected from the littoral zone of each lake, in the fall of 1981 and the spring of 1982, using electrofishing gear and dip nets. Fish were treated in the same manner as laboratory fish, except stomach contents were removed before weighing and freezing. Changes in body composition over winter were evaluated using the same set of statistical procedures used in evaluating changes observed in the laboratory. Water chemistry data for the lakes were obtained from samples analyzed by the Water Chemistry Laboratory of the Ontario Ministry of the Environment (OMOE), according to methods outlined in OMOE (1981).

Results

Starvation Effects

Comparisons between fish killed at the start of each experiment and fish killed after 6 wk of starvation revealed significant ($p < 0.01$) decreases in the mean wet weight and mean ash-free dry weight per individual (Table 3). In addition, significant ($p < 0.01$) decreases in the mean K concentration of the ash and increases in the mean Na and Ca concentrations of the ash were observed. No significant ($p > 0.05$) changes in the mean fork length per individual, mean ash weight per individual, or mean Cl concentration of the ash were noted with starvation.

Significant ($p < 0.01$) changes observed over winter in the three wild populations are consistent across lakes and largely parallel the changes observed in the laboratory starvation experiments: mean wet weight, mean ash-free dry weight, and mean K concentration declined; mean Ca concentration increased (Table 3); mean length and mean ash weight remained relatively constant. The changes in the Na and Cl concentrations observed in the field differed from those observed in the laboratory. In the field, mean Na and Cl concentrations declined significantly ($p < 0.01$). In the laboratory, the mean Na concentration increased, while the response of the mean Cl concentration was neither consistent nor statistically significant ($p > 0.05$).

Interactive Effects of Starvation and pH on Body Composition

There was no consistent trend linking low pH with greater losses of ash-free dry weight during starvation. Only in experi-

TABLE 2. Location, physical characteristics, water chemistry data, and sampling information for the three lakes supporting the wild smallmouth bass populations studied. For each lake, water chemistry data are the means of two independent samples: the first taken in Aug. 1981 and the second taken in Nov. 1982.

Descriptor	Lake		
	Kelly	Johnson	Lochlin
Location	45°15′N, 78°37′W	45°15′N, 78°37′W	44°57′N, 78°31′W
Area (ha)	99	151	30
Mean depth (m)	11.7	18.3	4.6
pH	6.86	6.76	5.70
Conductivity ($\mu\Omega \cdot cm^{-1}$ at 25°C)	31	31.2	24.5
Alkalinity (TIP, mg $CaCo_3 \cdot L^{-1}$)	1.67	1.37	0.33
Na ($mg \cdot L^{-1}$)	0.55	0.53	0.53
Cl ($mg \cdot L^{-1}$)	0.43	0.46	0.55
K ($mg \cdot L^{-1}$)	0.45	0.45	0.15
Ca ($mg \cdot L^{-1}$)	2.6	2.6	2.0
Dates fish sampled			
1981	Oct. 19	Oct. 20	Oct. 27
1982	May 17–28	May 20–29	May 20–29
n			
1981	20	20	20
1982	34	45	31
Mean length (cm)			
1981	6.1	6.0	7.3
1982	6.3	6.0	7.5
Length range (cm)			
1981	4.8–7.3	4.2–7.1	6.2–8.7
1982	4.6–7.4	4.5–7.4	6.1–8.9

TABLE 3. Statistically significant ($p < 0.01$) effects on body composition induced by starvation alone and additional significant effects induced by exposing starving fish to reduced pH levels. Wet weight, ash-free dry weight, and ash weight refer to absolute values for a fish of standard size (fork length = 6.4 cm); elemental concentrations refer to concentrations in ash derived from whole fish.

Effect	Lab or field data	Component	Observed change
Starvation	Lab	Wet weight	Decrease
		Ash-free dry weight	Decrease
		Na concentration	Increase
		K concentration	Decrease
		Ca concentration	Increase
Starvation	Field	Wet weight	Decrease
		Ash-free dry weight	Decrease
		Na concentration	Decrease
		K concentration	Decrease
		Ca concentration	Increase
		Cl concentration	Decrease
pH < 4.6	Lab	Wet weight	Decrease
pH < 4.6	Lab	Ash weight	Decrease
pH < 4.9	Lab	Na concentration	Decrease
pH < 4.6	Lab	K concentration	Decrease
pH < 4.6	Lab	Cl concentration	Decrease

ment 3 did the fish held at low pH levels have significantly ($p < 0.05$) lower ash-free dry weights than those fish held at higher pH levels. In contrast, there were consistent and significant (Table 3) trends in the data linking low pH with lower values for mean wet weight, mean ash weight, and the mean Na, Cl, and K concentrations in the ash. The data also suggested that exposure to reduced pH led to an increase in the Ca concentration in the ash. All of these effects became evident at about pH 4.5 and appeared to intensify at lower pH levels.

Figure 2 provides a quantitative picture of the changes taking place in the components of a fish of standardized length (6.4 cm), forced to exist on the energy stored in the ash-free dry weight fraction of its body. It also illustrates how these changes are influenced by exposure to low pH. Under moderate

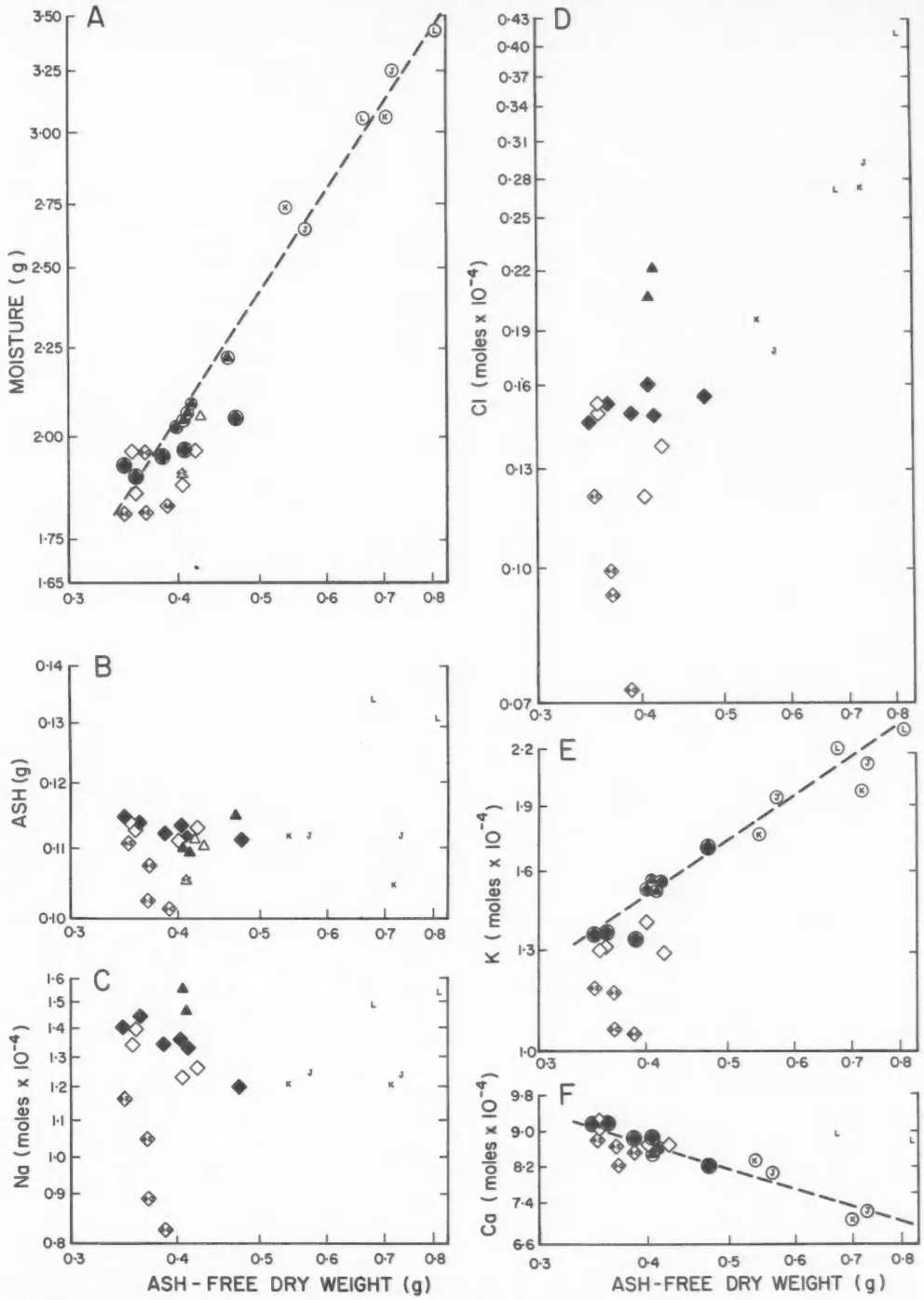

FIG. 2. Log–log relations between (A) moisture, (B) ash, (C) Na, (D) Cl, (E) K, (F) Ca, and ash-free dry weight. Points represent estimates of the absolute amount of each component in a fish of fork length 6.4 cm. Declines in ash-free dry weight are indicative of increasing starvation. Ordinates all follow the same logarithmic scale; therefore, the heights of the graphs indicate the overall variation observed in each component. Broken lines in Fig. 2A, 2E, and 2F were derived from least squares regression; points used in each regression are circled. For laboratory fish, closed symbols (▲, experiment 1; ◆, experiments 3 and 4) are for pH > 5.5 and open symbols are for pH < 5.5; for pH < 4.5, the actual value is given within the symbol. For wild fish, letters designate the lake (L = Lochlin, K = Kelly, J = Johnson).

pH conditions (pH > 5.5) in both the field and the laboratory, a decline in ash-free dry weight is accompanied by an increase in Ca and declines in both moisture and K. Starvation-induced decreases in ash-free dry weight were not accompanied by consistent changes in the other three components studied: ash, Cl, and Na.

All of the moisture data, from both the wild fish and the laboratory fish held at moderate (> 5.5) pH levels, closely ($r = 0.98$, $n = 16$, $p < 0.01$) followed the regression equation

$$M = 4.055(AFDW)^{0.762}$$

where M is moisture (grams per fish) and AFDW is ash-free dry weight (grams per fish) (Fig. 2A). The exponent in the equation is significantly less than 1.0, indicating that the amount of water per unit ash-free dry weight increased progressively with increasing starvation. Four of the five points derived from fish exposed to pH levels less than 4.5 fall below the regression line, suggesting that exposure to low pH may result in accelerated moisture loss in starving fish (Fig. 2A).

In contrast with the results for moisture at moderate (≥ 5.5) pH levels, no consistent relationship was observed between changes in ash weight and changes in ash-free dry weight (Fig. 2B). However, there is evidence that exposure to low pH leads to an abnormal loss of ash: values from laboratory fish exposed to low (< 4.5) pH levels lie well below all of the values from laboratory fish exposed to pH 4.6 or above (Fig. 2B).

There was little consistency in the response of Na content to reductions in ash-free dry weight (Fig. 2C). There was also considerable variation in mean Na levels across data sets: fish from one lake (Lochlin Lake) contained much higher Na levels than fish from the other two lakes, and fish from experiment 1 contained more Na than fish from experiments 3 and 4. At lower pH (below 5.0), an abnormal loss of Na was observed. The extent of this loss increased progressively with decreasing pH (Fig. 2C).

There was a general tendency for Cl content to decline during starvation at moderate (> 5.5) pH levels. However, both the rate of decline and the average level of Cl in the body varied considerably from data set to data set (Fig. 2D). At lower pH (below 5.0), there was a progressive increase in the normal rate of Cl loss with starvation (Fig. 2D).

At moderate pH levels (> 5.5), K content declined progressively as ash-free dry weight declined. Data from the wild fish and all data from laboratory fish held at moderate (> 5.5) pH levels closely ($r = 0.974$, $n = 14$, $p < 0.01$) followed the regression equation

$$K = 0.269(AFDW)^{0.657}$$

where K is potassium (millimoles per fish) (Fig. 2E). The exponent is significantly less than 1.0, indicating that the amount of K per unit ash-free dry weight increased progressively with increasing starvation. As pH fell below 5.0, there was a progressive increase in the normal rate of K loss during starvation (Fig. 2E).

At moderate pH levels, Ca content increased as starvation progressed (Fig. 2F). Data from two wild populations and all data from laboratory fish held at moderate (> 5.5) pH levels closely ($r = -0.961$, $n = 12$, $p < 0.01$) followed the regression equation

$$Ca = 0.67(AFDW)^{-0.302}$$

where Ca is calcium (millimoles per fish) (Fig. 2F). The average Ca content of the fish from one lake (Lochlin Lake) was much higher than that found in fish from other locations but, here too, Ca content increased as ash-free dry weight declined. All of the data points from fish exposed to low (< 4.5) pH levels lie well below the Ca/ash-free dry weight regression line, suggesting that exposure to low pH leads to a reduction in the normal rate of Ca accumulation during starvation (Fig. 2F).

Discussion

Many studies of the effects of starvation on the body composition of fish have been published in the last 30 yr (see Love 1970, 1980 for reviews of studies published prior to 1978). A number of general patterns are evident in this work. Losses of lipid and other carbohydrate energy stores are common along with concomitant increases in the water content of various tissues (Johnston and Goldspink 1973; Stirling 1976; Jobling 1980; Love 1980; Toneys and Coble 1980; Arunachalam and Reddy 1981; Mustafa 1983; Reinitz 1983). The latter is usually interpreted as reflecting an increase in the relative size of the extracellular space due to lipid loss. Muscle protein, particularly protein associated with the contractile fibres of white muscle, is often mobilized as an additional energy source (Creach and Serfaty 1974; Moon and Johnston 1980; Johnston and Goldspink 1973; Stirling 1976; Moon 1983a, 1983b; Beardall and Johnston 1983; Love 1980). Concomitant changes in muscle structure include a decline in the cross-sectional area and volume of contractile fibres (Beardall and Johnston 1983; Moon 1983b; Creach and Serfaty 1974), a decline in the total mitochondrial volume of muscle cells (Beardall and Johnston 1983; Moon 1983b), a decline in the vascularization of muscle tissue (Beardall and Johnston 1983), and shrinkage of muscle cells with a consequent increase in the extracellular space between cells (Creach and Serfaty 1974; Love 1980). The changes listed above lead to an increase in the relative size of the extracellular space in muscle tissue and an increase in the water content of muscle cells. These changes, in turn, lead to a considerable increase in the water content of muscle tissue.

Changes in the relative sizes of the extracellular and intracellular spaces have been invoked to explain observed changes in the Na, Cl, and K content of starving fish (Love 1970, 1980). Since Na and Cl are primarily confined to the extracellular space and K is primarily confined to the intracellular space (Holmes and Donaldson 1969; Love 1970), one would expect the Na and Cl concentrations in the tissues of starving fish to increase and the K concentration to decrease. Such changes have been reported in a number of studies of muscle tissue (Moon 1983b; Kanevskii 1981; Soutter and Huggins 1977; Sutton 1968). Our observations on starvation-induced changes in the water and elemental content of whole fish were qualitatively similar; the amount of water per fish declined less rapidly than dry weight so that water content, on a dry weight basis, increased progressively; Na per fish increased (laboratory) or remained relatively constant (field) so that Na concentration, on a wet or dry weight basis, increased; K per fish declined progressively so that K concentration, on a wet weight basis, either decreased (laboratory) or remained relatively unchanged (field). K concentration on a dry weight basis increased in both the laboratory and the field, but this probably reflects the tendency for the significant amounts of K associated with skeletal material to mask shifts in the K concentration of soft body tissue.

The fact that the amount of Na per fish actually increased

(laboratory) while the total moisture content per fish declined suggests a greater accumulation of Na than that necessary to maintain isotonicity in an enlarged extracellular space. Similar observations were made by Meyer et al. (1955) and Creach and Serfaty (1974) who both suggested that some of this extra Na partially replaces K lost from the intracellular space. In experiments 3 and 4, the rate of decline in K (Fig. 2E) is essentially identical to the rate of increase in Na (Fig. 2C). This suggests that, under the conditions existing during these experiments, some exchange of Na for K may have occurred.

In our work on whole-body composition, we did not find the parallelism between Cl and Na behavior reported by authors working on muscle alone (Sutton 1968; Love 1980). Cl concentration, on a wet or dry weight basis, declined in the wild populations, while in the laboratory experiments there was a moderate increase. Our data, therefore, are not consistent with the hypothesis that starvation-induced shifts in these elements can be explained on the basis of changes in the relative sizes of extracellular and intracellular spaces. This discrepancy could arise if the dynamics of Na and Cl in muscle are masked by other processes, operating at the level of the whole fish. However, Houston and Mearow (1979) have shown that, for most of the major tissues in fish, the Cl space provides a much more accurate measure of the extracellular space than the Na space. Therefore, it may be more appropriate to regard shifts in Cl concentration as indicative of shifts in the relative sizes of cellular spaces, while shifts in Na concentration are seen as indicative of the combined effect of changes in both the size of cellular spaces and the distribution of Na between those spaces.

A few reports in the literature parallel our observation of a systematic increase in Ca absolute amount and/or concentration (Reufs and Weinland 1913, cited in Meyer et al. 1955; Moon 1983b). Moon (1983b) interpreted his observation that Ca and Na concentrations increased in muscle and declined in plasma of eels (*Anguilla rostrata*) during starvation as indicative of a progressive decline in the effectiveness of osmoregulation during starvation. This interpretation is supported by observations in fish (Jurss et al. 1983) and other organisms (rats, Machado et al. 1971) that Na-K ATPase activity progressively declines as starvation procedes and by the observation, in mammals, that starvation is accompanied by electrolyte imbalance (Creach and Serfaty 1974). This interpretation of the changes in elemental composition induced by starvation is of particular interest when we consider the impact of exposure to low pH.

Our results do not support the hypothesis that chronic exposure to low pH conditions leads to a significant increase in metabolic costs. However, they do demonstrate that some of the effects of low pH exposure on elemental composition are, in essence, an accentuation of the changes that accompany starvation: moisture and K losses are accelerated. In addition, outright reversals of starvation effects occur: abnormal losses in Cl, Na, and Ca are induced. Such changes are the result of impaired osmoregulatory function (Wood and McDonald 1982). Low-pH toxicity has itself been explained in terms of a cardiovascular collapse induced by osmoregulatory failure. If we accept this explanation of pH toxicity and the hypothesis that starvation is accompanied by a progressive weakening of the osmoregulatory system, it follows that starvation should be accompanied by a reduction in tolerance to low pH conditions. Evidence for this effect has recently been presented by Kwain et al. (1984) who showed that the pH LC_{50} (96 h) of young-of-year smallmouth bass increased progressively as starvation time increased.

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Transport of ^{60}Co between Water and Sediments in a Small Shield Lake

R. Jack Cornett and Ivan L. Ophel[1]

Environmental Research Branch, Chalk River Nuclear Laboratories, Chalk River, Ont. K0J 1J0

Cornett, R. J., and I. L. Ophel. 1986. Transport of ^{60}Co between water and sediments in a small shield lake. Can. J. Fish. Aquat. Sci. 43: 877–884.

Low levels of ^{60}Co, discharged from a waste management area, have flowed into a small shield lake over a period of 22 yr. Constructing a mass balance using measured waterflows, measurements of ^{60}Co activities in the inflow, in the bottom sediments, and in the lake outlet provides a unique record of the isotope's behaviour. The long-term, annual, and seasonal movements of ^{60}Co between the water, sediments, and the outflow have been examined and compared. An instantaneously mixed, single reservoir model with constant parameters accurately simulated the average annual variations in ^{60}Co activity in the water and in the sediments. The lake sediments were the major sink for ^{60}Co. More than 90% of the ^{60}Co present in the lake system at any one time was found in the sediments. However, less than half of the total ^{60}Co inputs were retained in the sediments over the 22-yr period. The remainder left the lake through the outflow. The fractional rate of ^{60}Co deposition in the sediments was independent of the rate of ^{60}Co inputs and independent of the ^{60}Co activity in the lake sediments. Seasonal changes in ^{60}Co concentrations in the lake water were very large. Spring and summer concentrations were often 50–500% lower than predicted from a model that simulated annual average concentrations. The bias was likely due to rapid removal of ^{60}Co by increased scavenging of the isotope by particulates. During the winter, ^{60}Co concentrations in the lake water were greater than expected, probably due to the exclusion of ^{60}Co from lake ice, incomplete mixing of the inflow with the lake water, or release of ^{60}Co from the sediments. These seasonal variations in the ^{60}Co activity were accurately simulated by a single reservoir model using different removal rates for the summer and winter periods.

De petites quantités de ^{60}Co, provenant d'une zone de gestion des déchets, se sont ecoulées dans un petit lac du Bouclier pendant 22 ans. En établissant un bilan de masse basé sur des débits d'eau mesurés, on a relevé les concentrations de ^{60}Co dans l'eau d'alimentation, dans les sédiments de fond et dans le réservoir du lac, constituant ainsi un dossier unique sur le comportement de l'isotope. Les mouvements à long terme, annuels et saisonniers du ^{60}Co entre l'eau, les sédiments et le déversoir ont été examinés et comparés. Un modèle de réservoir unique à mélange instantané, présentant des paramètres constants, a permis de simuler avec beaucoup de précision les variations annuelles moyennes de concentrations de ^{60}Co dans l'eau et dans les sédiments. C'est surtout dans les sédiments du lac qu'on a retrouvé le ^{60}Co. Plus de 90 % du ^{60}Co présent dans le système lacustre en tout temps se trouvaient dans les sédiments du lac. Toutefois, moins de la moitié des apports totaux de ^{60}Co ont été retenus dans les sédiments pendant la période de 22 ans. Le reste est sorti du lac par le déversoir. Le taux fractionnaire de dépôt de ^{60}Co dans les sédiments était indépendant du taux d'apport en ^{60}Co et de la concentration de ^{60}Co dans les sédiments du lac. Les variations saisonnières des concentrations de ^{60}Co dans l'eau du lac étaient très importantes. Au printemps et en été, les concentrations était souvent inférieures de 50 à 500 % à celles prévues par un modèle de simulation des concentrations annuelles moyennes. L'écart était probablement dû à l'élimination rapide du ^{60}Co par nettoyage accru de l'isotope par des particules. En hiver, les concentrations de ^{60}Co dans l'eau du lac étaient supérieures à celles prévues, probablement à cause de l'exclusion de ^{60}Co dans la glace du lac, du brassage incomplet de l'eau d'alimentation avec l'eau du lac ou de la libération du ^{60}Co des sédiments. Ces variations saisonnières de l'activité du ^{60}Co ont été simulées avec précision dans un modèle de réservoir unique en utilisant différents taux d'élimination pour l'été et l'hiver.

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Contaminants input into freshwaters may act conservatively or react with other constituents present in the lake. Trace metals and radionuclides frequently sorb onto particles in the water or at the sediment–water interface (e.g. Hesslein et al. 1980; Wahlgren et al. 1980; Forstner and Wittman 1981). As a result of this interaction the concentration of an element in the water decreases and it accumulates in the bottom sediments.

Removal rates of several elements from water and their accumulation in lake sediments have been determined by two methods: (1) measuring changes in the concentration of tracers added to lakes in short-term (less than 1 yr) experiments (e.g. Hesslein et al. 1980; Schindler et al. 1980; Santschi et al. 1983, 1986) and (2) determining the distribution of an element

[1]Deceased, formerly with Environmental Research Branch.

many years after it was input to the lake (e.g. Edgington et al. 1976; Alberts and Wahlgren 1981; Brunskill et al. 1984; Cornett et al. 1984). These two types of study provide information about processes with very different time constants: rapid, short-term seasonal events versus long-term integrated annual or multiyear processes. Rarely is it possible to compare the two types of studies on a single system (Wahlgren et al. 1980). Usually data are incomplete, the tracer decayed to unmeasurable levels, or insufficient time has elapsed to examine long-term events.

In this paper we describe a unique set of ^{60}Co measurements, collected over 22 yr, which overcome many of the problems mentioned above. ^{60}Co activity has been measured in the inflow, in the outflow, and in the bottom sediments of Perch Lake, a small dystrophic lake located on the Canadian Shield. These analyses permit comparison of the ^{60}Co mass balance over single seasons and over relatively long-time periods (>10 yr) as the inputs of ^{60}Co and the distribution of ^{60}Co between the sediments and the water change.

Methods

Perch Lake is a small (area 45 ha), shallow (mean depth 2 m), dimictic, dystrophic, softwater shield lake (Barry 1975) located on the property of Atomic Energy of Canada Limited (Ontario, Canada, 77°22′W, 46°2′N). Since 1961 the lake has received small amounts of ^{60}Co via two inlets flowing from waste management areas (Killey et al. 1984). Water entering the lake has been monitored for ^{60}Co at approximately weekly intervals since 1961. Since 1969 the lake water and/or the outlet were sampled also.

One-litre inflow samples or 20-L lake samples were acidified with HCl and boiled down to 100 mL. These samples were counted on a NaI detector attached to a single-channel or multichannel analyzer. Water samples collected after 1971 were acidified and evaporated on sheets of polyethylene under heat lamps (Grummitt and Lahaie 1978). Since 1972 the weekly samples were pooled into a single monthly or quarterly composite sample before analysis. The polyethylene and the residues were folded and pressed into a pellet with constant geometry. Then they were counted using a Ge(Li) detector coupled to a multichannel analyzer. The counters were standardized using solutions of ^{60}Co of known activity prepared like the samples.

Nine sediment samples were collected along a single east–west transect across the lake to the outlet using a 15-cm Ekman dredge in September 1969 (Ophel and Fraser 1973). During August 1982, 31 sites were cored using a modified KB corer with 7-cm inside diameter lucite core tubes. The sites were chosen using a stratified random sampling design distributed over the entire lake bottom (see Evans et al. 1986). Cores were collected in the littoral zone by adding a brass weight to the corer so that it could penetrate into sandy sediments or pass through macrophyte roots. There was no area where cores could not be collected. Sediment from the whole 0 to ~15-cm layer below the sediment–water interface (1969) or the entire 0 to 20-cm layer (1982) was homogenized, dried, ground, and then pressed into a constant cylindrical geometry. Concentrations of ^{60}Co in the samples were determined by gamma-ray spectroscopy using a NaI detector. Spiked sediments (of the same densities and geometry as the samples) were counted to measure the counting efficiency of the samples. The activity of ^{60}Co per unit area of lake bottom was calculated by multiplying the activity per gram by the mass of the core and dividing by the core area.

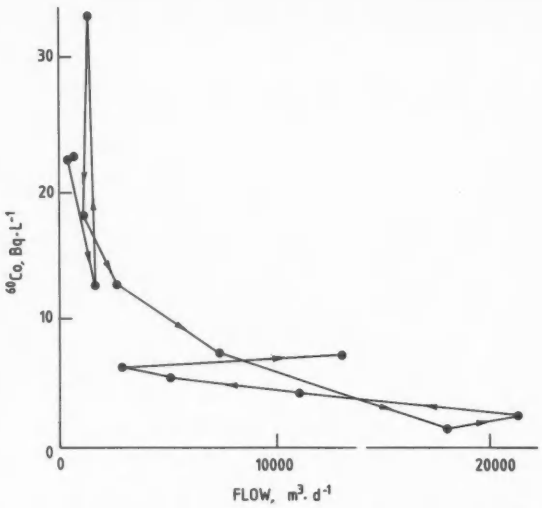

FIG. 1. Relationship between ^{60}Co concentrations and hydrologic flow in the inlet stream during the spring of 1971. The arrows join sampling points approximately 1 wk apart starting February 28 and continuing to May 8.

The input of ^{60}Co to the lake was estimated from measured stream flows and ^{60}Co concentrations. Stream flow was measured using V-notch or broad-crested weirs (Barry et al. 1978). From 1961 to 1967, weekly measurements of stream stage were taken. Since 1967 the flows have been monitored continuously with stage recorders. The activity of ^{60}Co input to the lake was calculated as the integral of the concentrations measured in weekly samples from the inlet multiplied by the flows measured on the same dates. This method of calculation introduced a systematic overestimation of the inputs of cobalt when the concentration measured in inflow samples pooled into a composite sample was multiplied by the average flow during the period. This occurred because the concentration of ^{60}Co in the inflowing stream and the volume of stream discharge were correlated; the regression was a negative nonlinear relationship (Fig. 1). A correction for the bias was derived from periods when discrete samples were collected. This correction was applied to all data collected since 1973.

To determine T_s, the partial residence time for ^{60}Co removal from the water to the sediments, the water column of Perch Lake was defined as an unstratified, continuously mixed reactor (Lerman 1979). Then

$$(1)\quad \frac{dC}{dt} = \frac{J}{V} - \frac{C}{T_w} - \frac{C}{T_s} - \lambda C$$

where J is the rate that the ^{60}Co is discharged into the lake (becquerels per day), C is the concentration of ^{60}Co in the lake water (becquerels per litre), V is the lake volume (litres), T_w is the hydraulic residence time of the lake (days), T_s is the partial residence time for removal of ^{60}Co from the water to the bottom sediments (days), and λ is the rate constant for radioactive decay (per day). Using equation 1 in a finite difference form, a Basic computer program simulated the movement of ^{60}Co between the water, the lake outflow, and the sediments. T_s was determined by three methods. First, T_s was adjusted until the sediment burden predicted by the simulation agreed with the burden measured in 1969 or 1982. In the second method,

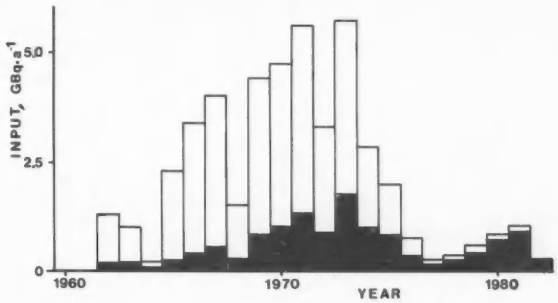

FIG. 2. Annual inputs of ^{60}Co to Perch Lake. The shaded portion is the input after a decay correction to September 1982.

sedimentation of ^{60}Co was estimated as the difference between the inputs of ^{60}Co and the activity discharged through the outlet. Finally, T_s was determined by simulating annual average or seasonal ^{60}Co concentrations measured in the lake water using a least squares fit.

Results and Discussion

Input of ^{60}Co

The ^{60}Co entering Perch Lake originates from a waste management area located in the Perch Lake drainage basin. ^{60}Co emplaced in the management area migrates through a shallow overburden groundwater aquifer and eventually flows into streams. The mobility of ^{60}Co in the groundwater system is enhanced because a significant fraction of the nuclide is complexed with low molecular weight organic compounds. The persistence of the ^{60}Co complex in surface waters is uncertain because the complex is decomposed in sunlight (Killey et al. 1984).

During the period 1961–82 inclusive, 12.1 GBq of ^{60}Co (decay corrected to September 1982) was discharged into Perch Lake (Fig. 2). There were very few records of Co measurements in the inflows prior to 1961. Limited evidence suggests that earlier ^{60}Co inputs were much lower than inputs after 1961 (Killey et al. 1984). A large fraction of these inputs would be decayed by 1969 or 1982. Therefore this uncertainty in the mass balance introduces an error in the total loading estimates of less than 2%. The input of ^{60}Co was not constant through time (Fig. 2). The concentration of ^{60}Co in the inflow and the total quantity of Co discharged increased from 1961 to 1973. Loading decreased in subsequent years. During this period, the annual lake's hydrologic residence time ranged from 0.31 to 0.77 yr and averaged 0.5 yr (Barry et al. 1978).

Accumulation of ^{60}Co in Lake Sediments

The lake sediments accumulated ^{60}Co. In 1969 and 1982, the sediments contained 93 and 98% of the total ^{60}Co present in Perch Lake.

^{60}Co was widely distributed over the lake bottom in both sets of cores (Fig. 3). ^{60}Co activity in the sediments was not significantly higher near the source inlet. The activity of ^{60}Co in sandy nearshore sediments was very similar to that measured in the organic rich gyttja in the lake centre (Ophel and Fraser 1973).

The depth distribution of ^{60}Co was examined in cores of gyttja and sand (Fig. 4). In both 1969 and 1982 almost all of the activity was confined to the upper 15 cm of gyttja. In sandy nearshore cores all ^{60}Co activity was found to be in the upper

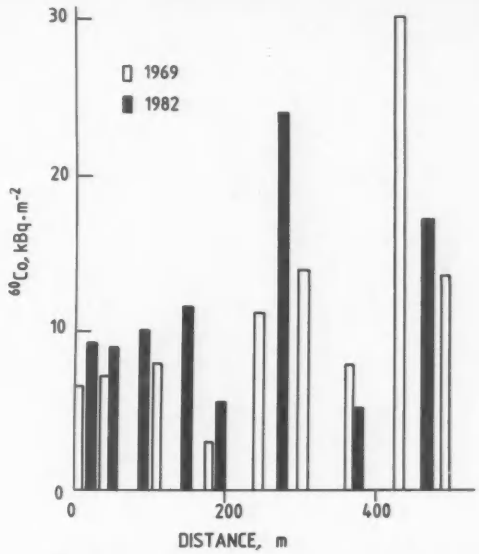

FIG. 3. ^{60}Co activity in sediment cores collected along a transect located 100 m offshore and parallel to the lake's north shore. Distance is measured from the west shore. The inflow is located on the north shore approximately 200 m from the west shore. In 1982, cores were collected at 23 additional sites in the lake.

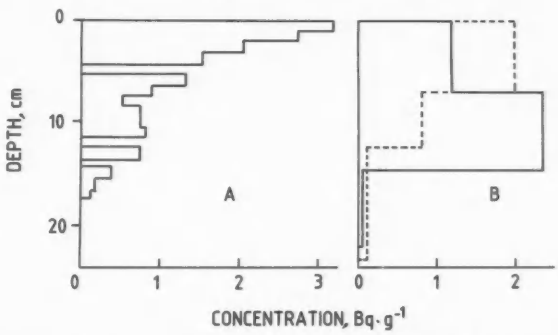

FIG. 4. ^{60}Co concentration profiles in sediment cores collected in (A) 1982 and (B) 1969. Samples were collected on the transect shown in Fig. 2 at a site about 300 m from the west shore. The two profiles shown in Fig. 4B were collected from soft gyttja (solid line) and from inorganic sands (broken line) nearer to the west shore.

10 cm. ^{60}Co was found much deeper in all cores than expected from knowledge of the bulk accumulation rate of dry sediment. The depth distribution of ^{60}Co was very poorly correlated with the history of ^{60}Co inputs (Fig. 2). Since there was no evidence of a mixed layer in the core sectioned in 1-cm slices (Fig. 4), we hypothesize that ^{60}Co must diffuse within the pore water.

In both 1969 and 1982 the frequency distributions of ^{60}Co activity in the cores were log-normal (Fig. 5). These distributions, similar to those of other sediment contaminants (Forstner and Wittman 1981), suggest that the geometric means are the best estimates of activity in the sediments. The geometric means and 95% confidence intervals were 9500 Bq·m^{-2} (8100–11 400, $N = 9$) and 8600 Bq·m^{-2} (7300–10 200, $N = 31$) in 1969 and 1982, respectively. Although the two sets of cores were not taken at identical locations, the areal

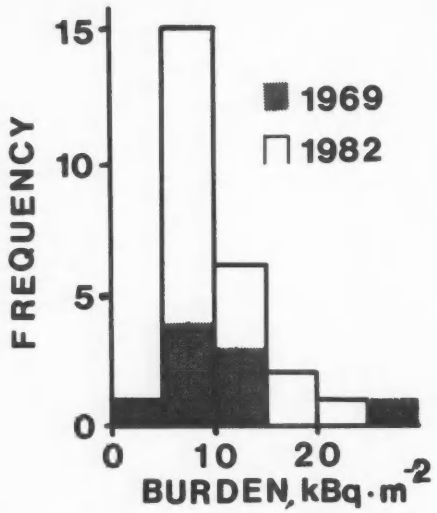

FIG. 5. Frequency histogram plotting the number of cores against the ^{60}Co burden in the core.

distribution of ^{60}Co was sufficiently uniform between years, and the sampling areas overlapped. Therefore a comparison was justified (Evans et al. 1985). The two sediment burdens were not statistically different ($P > 0.05$, $t = 0.30$, $N = 40$). However, by 1982, 80% of the ^{60}Co measured in the sediments in 1969 would have decayed (half life 5.27 a). Therefore sufficient ^{60}Co accumulated in the sediments during that 13-yr period to approximately balance the loss by radioactive decay.

Comparison of ^{60}Co Loading and Accumulation in the Sediments

In Perch Lake more than 90% of the ^{60}Co present in the sediments, water, and fauna was found in the lake sediments. This distribution is consistent with the distribution of other particle-reactive contaminants (e.g. Forstner and Wittman 1981). However, the distribution of ^{60}Co does not imply that all of the ^{60}Co input into Perch Lake accumulated in the lake sediments. Comparing the ^{60}Co inputs with the geometric average burdens shows that the sediments retained only approximately 38 and 31% of the total decay-corrected ^{60}Co inputs to the lake in 1969 and 1982, respectively. These values are not statistically different ($P > 0.05$, $t = 0.74$).

The observation that less than 40% of the ^{60}Co input into Perch Lake accumulated in the sediments was surprising initially. This percentage was much smaller than the fractional retention of other particle-reactive nuclides (e.g. ^{137}Cs and ^{239,240}Pu) measured in the Laurentian Great Lakes (Alberts and Wahlgren 1981). However, the retention of ^{60}Co in Perch Lake was very similar to the annual retention of ^{210}Pb in the sediments of this lake (39%) and other small shield lakes (Cornett et al. 1984). The different retentions in different lakes result from their different water renewal times. The water renewal time for Perch Lake was 0.5 yr, while the Great Lakes flush more slowly (3.3–100 yr).

The ^{60}Co in the sediments has accumulated over many years. To examine processes occurring on a shorter time scale, the amount of ^{60}Co lost from the water column and deposited in the sediments per annum was calculated by comparing ^{60}Co activities in the inflowing and outlet streams. The fraction of the annual ^{60}Co inputs retained in the lake sediments was defined as the difference between the input and the output activities divided by the input. From 1970 to 1982, 45 ± 10% of the annual inputs were deposited in the sediments (Fig. 6). Fractional retention did not change systematically during this period and was not correlated with the annual amount of ^{60}Co input. This estimate of retention was higher than the estimates derived from the sediment budgets. At present we cannot explain this difference.

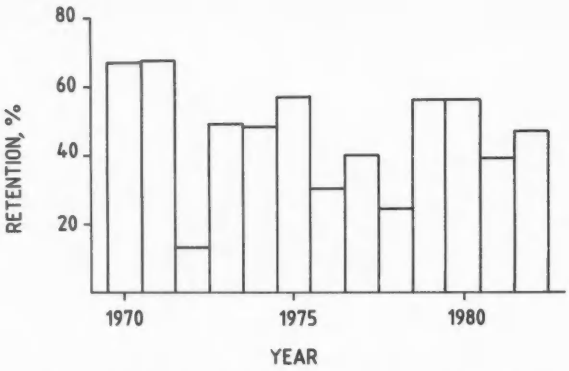

FIG. 6. Annual percent of ^{60}Co inputs retained in the lake sediments estimated from the input–output budget. Estimates of retention calculated from the accumulation of ^{60}Co in the sediments were 38 and 31% in 1969 and 1982, respectively.

Partial Residence Time of ^{60}Co in the Water

The fractional retention of ^{60}Co was the result of two variables: the hydrologic flushing rate of the lake and the removal rate of ^{60}Co from the water to the sediments. We have separated these two variables by simulating the measured sediment activities using equation 1. To account for the sediment activities reported above, the partial residence time of ^{60}Co in the water was 0.8 yr prior to 1969. The T_s value calculated using the 1982 sediment burden was 1.1 yr. These two values of T_s, which describe the partial residence time of the nuclide in the water column, were not statistically different during periods of increasing (to 1969) and decreasing loading (to 1982) ($P > 0.05$, $t = 1.1$).

The influence of T_w and T_s on the accumulation of nuclides in lake sediments can be illustrated by comparing the retentions and T_s values of nuclides in different lakes. Although the fractional retentions of nuclides vary from lake to lake, the T_s value for ^{60}Co sedimentation was very similar to rate constants describing ^{239}Pu and ^{137}Cs sedimentation in Lake Michigan (Edgington et al. 1976), ^{210}Pb in Lake Huron (Durham and Joshi 1980), and ^{137}Cs in Lake Ulkesjon (Carlsson 1978). The remarkably similar behaviour of these different elements in different lakes suggests that future analysis should focus upon the partial residence time of elements in the water. Any comparison of fractional retentions is strongly influenced by the hydrologic flushing rates of the lakes (Kirchner and Dillon 1975). Extrapolating these observations to other lakes with flushing rates greater than one per annum suggests that <50% of the annual input of a reactive element will be deposited in the lake sediments.

An independent estimate of T_s was made by simulating the concentrations of ^{60}Co in Perch Lake. Average annual ^{60}Co

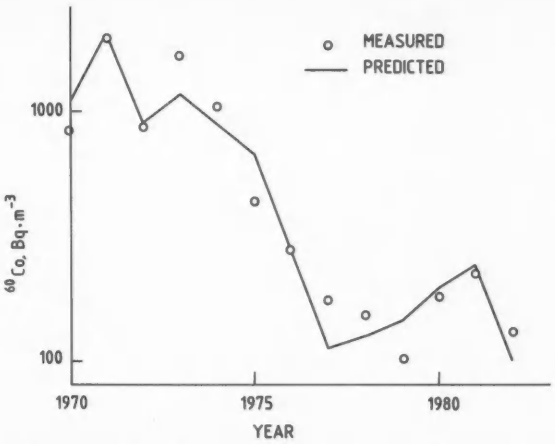

FIG. 7. Comparison of annual average ^{60}Co concentrations measured in the lake water with values predicted using a single reservoir model with a constant T_s value of 0.52 yr.

concentrations measured in the lake and in the outlet were compared with values predicted using a finite difference approximation to equation 1 (Fig. 7). The T_s value defined by the least squares fit was 0.52 yr. This simulation correctly predicted the decrease in ^{60}Co concentrations produced by the decreased input of ^{60}Co. Scatter diagrams showed that the deviations between the predicted and observed concentrations were random. There was no correlation between these deviations and the amount of ^{60}Co input into the lake per annum ($R = 0.41$, $P > 0.05$); nor were the residuals correlated with the year the measurements were made ($R = 0.03$, $P > 0.05$). From these observations we conclude that the annual average ^{60}Co concentration was adequately simulated by a model using a constant transfer of ^{60}Co from the water to the lake sediments. Over this 12-yr period, T_s was not dependent on the amount of ^{60}Co input into the lake.

Seasonal Transfer of ^{60}Co between Water and Sediments

The simulations and models described in earlier sections were designed to examine the movement of ^{60}Co through Perch Lake over annual or longer time periods. These models adequately predicted concentrations of ^{60}Co as the input of ^{60}Co changed over the years. However, the analyses did not accurately describe the dynamic short-term or seasonal changes in ^{60}Co concentrations. Often, ^{60}Co concentrations change by more than one order of magnitude over a period of months or a single season (Fig. 8). These changes in activity were not completely explained by changes in the amount of ^{60}Co input to the lake. Short-term changes in ^{60}Co concentrations were not simulated by a model using an annual average T_s value.

The fluctuations in ^{60}Co concentration were systematic. During the winter, ^{60}Co concentrations increased rapidly whereas during the summer, concentrations in the water decreased. As a result there was a seasonal bias in the predicted ^{60}Co concentrations. During the winter, predicted ^{60}Co values were significantly less than the measured values (sign test, $\chi^2 = 10.2$, $P < 0.01$, method of Snedecor and Cochran 1967). The opposite trend was observed during the summer. Of 41 ^{60}Co measurements only 8 were greater than the predicted values. This systematic bias was significantly different from the expectation (sign test, $\chi^2 = 14.0$, $P < 0.01$).

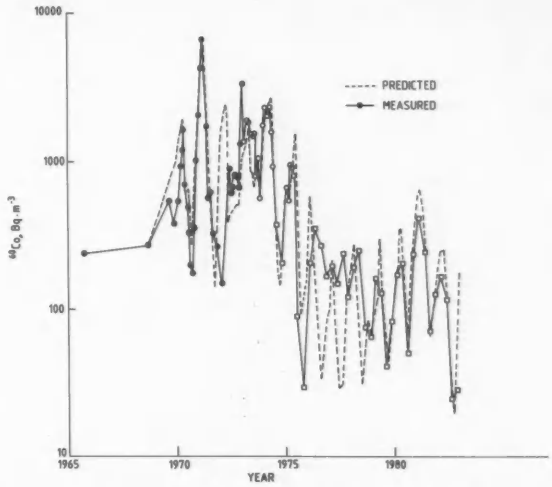

FIG. 8. ^{60}Co concentrations measured in the water or lake outflow plotted against values predicted using a seasonal simulation with a T_s value of −1.5 yr during the winter and 0.21 yr during the summer. Solid circles were measured weekly, and monthly averages were calculated. The open circles and squares are monthly and quarterly composite measurements, respectively.

Monthly ^{60}Co concentrations, measured from 1970 to 1982, were simulated more accurately using separate T_s values for the summer (May−October) and for the winter periods (November−April). Using a least squares fit, the best estimates of T_s during the winter and summer periods were −0.67 and 0.21 yr, respectively. This seasonal model explained significantly more residual variation than the model employing an annual average T_s value ($F = 1.95$, $N = 85$, $P < 0.01$).

During the winter when Perch Lake was covered with ice, ^{60}Co concentrations were best simulated by a model with a negative T_s value. ^{60}Co concentrations increased more rapidly than can be expected by ^{60}Co inputs through the inlet. Three possible explanations for the increasing ^{60}Co concentrations during the winter are as follows.

(1) ^{60}Co was excluded from ice as the lake ice forms. The formation of ice coupled with freeze-out would have increased ^{60}Co concentrations in the remaining water. The smaller volume of lake water receiving inputs of ^{60}Co through the inlet would also result in increased ^{60}Co concentrations in the lake water. Although the thickness of ice covering Perch Lake has not been mapped in detail, it was estimated to be 0.5 m in thickness at the end of January. Since Perch Lake is shallow ($Z = 2$ m), the growth of ice corresponds to a volume change of $0.25\% \cdot d^{-1}$. This change is comparable with the $0.41\% \cdot d^{-1}$ increase in ^{60}Co concentrations calculated from the simulations mentioned above. Therefore, freeze-out of ^{60}Co and the reduced lake volume could explain the changes in concentration that were observed.

(2) The simulation models used earlier all assumed that during the winter the lake was instantaneously mixed. If ^{60}Co input into Perch Lake did not mix completely, then concentrations measured at the centre of the lake or in the outflow would not correctly estimate the mean concentration of ^{60}Co in the lake water. During periods of ice cover, water from the outlet was especially prone to overestimate lake concentrations. This could occur because the colder, lighter inflowing waters did not completely mix with the lake before flowing to

the outlet. During the winter the inflow of water into Perch Lake was sufficient to influence outflowing ^{60}Co concentrations. The average hydrologic residence time of water in the lake is 1.7 yr during the first 5 mo of ice cover. Inhomogeneities in mixing have been documented in Perch Lake and in other small lakes using ^{3}H as an indicator of water movements (Barry and Jay 1975; Bergman 1982). Unfortunately, these estimates are not sufficiently quantitative to compare the winter T_s value with the degree of inhomogeneity.

(3) The increased ^{60}Co concentrations under the ice could also have resulted from the remobilization of ^{60}Co from the lake sediments. ^{60}Co is released from sediments under anoxic conditions (Hesslein et al. 1980). Under the ice, oxygen concentrations measured in the water were very low or anoxic (McMahon 1966). However, our knowledge of ^{60}Co release rates under anoxic conditions is not sufficient to compare with the observed measures of T_s reported above.

With our existing data, we cannot distinguish between these possible interpretations of the changes in ^{60}Co concentrations during the winter. One or a combination of mechanisms may be responsible for the increases in ^{60}Co concentrations that we have measured. Further experiments are required to analyse this problem.

Changes in ^{60}Co concentrations during the summer were opposite to those measured in the winter. ^{60}Co concentrations decreased rapidly during the ice-free period (Fig. 8), and the average value of T_s was estimated to be 0.21 yr. A mechanistic explanation of the increased rate of ^{60}Co removal from the water has not been tested. We hypothesize that the change resulted from increased productivity, particle concentrations, and organic sedimentation during the summer months. Several studies demonstrated that the flux of particulate organic matter and nutrients to the sediments increases during the summer (e.g. Prepas and Rigler 1981; Rigler 1975; Bloesch 1974). Although variations in the sedimentation of trace elements have received less attention, seasonal changes in the ^{239,240}Pu and ^{137}Cs removal rates were documented in Lake Michigan (Wahlgren and Marshall 1975; Wahlgren et al. 1980). In Fayetteville Green Lake, the removal rate of ^{137}Cs also increased during the summer (Brunskill et al. 1984). Clearly, the seasonal changes in the removal rate of trace elements must receive more attention before accurate seasonal models can be developed.

The summer T_s value measured in Perch Lake was approximately three times longer than the T_s value (0.076 yr) calculated by Hesslein et al. (1980) after ^{60}Co was added to the epilimnion of a small shield lake. The difference between the two results may reflect physical, chemical, or biological differences between Perch Lake and ELA-224 Lake. However, the difference may also be attributed to the different chemical form of ^{60}Co inputs. ^{60}Co was added to ELA-224 in a dilute HCl acid solution as cobalt chloride. In contrast, a significant fraction of ^{60}Co flowing into Perch Lake is complexed by low molecular weight organics (Killey et al. 1984). Although this complex is decomposed in sunlight, the behaviour of the Co-complex appears to be different from that of inorganic ^{60}Co (Killey et al. 1984; R. J. Cornett, unpubl. data). Additional experiments comparing the removal rates of different species of Co isotopes are required.

Remobilization of ^{60}Co from the Sediments

The simulation models employed in earlier sections of this paper assume that the net loss of cobalt is from the water to the sediments and that there is no release of ^{60}Co from the sediments back to the water. If these assumptions are correct, then the transfer of ^{60}Co from the water to the sediments can be described by

$$(2)\quad \frac{dS}{dt} = \frac{V \cdot C}{T_s} - \lambda S$$

where S is the ^{60}Co activity in the sediments (becquerels) and the other variables were defined in equation 1.

However, laboratory experiments have shown that ^{60}Co can desorb from particles (Santschi et al. 1983). Since desorption can occur in the laboratory, it may also occur in the lake. To evaluate the significance of remobilization of ^{60}Co from the sediments, we have considered an alternative formulation of the sediment−water transfer:

$$(3)\quad \frac{dS}{dt} = \frac{V \cdot C}{T_s} - \frac{S}{T_r} - \lambda S$$

where T_r is the partial residence time for transfer of ^{60}Co in the sediments back to the water (days) and the other variables were defined earlier.

This equation describes the sediment water transfer as two processes: a transfer from the water to the sediments and a transfer from the sediments back to the water. Both fluxes depend on the activity of ^{60}Co in the respective compartments. A comparison of equations 2 and 3 suggests that two methods can be used to examine the possibility that ^{60}Co was released from the sediments to the water in Perch Lake. First, equation 3 can be substituted into a modified version of equation 1 and the concentrations of ^{60}Co in the water can be simulated. If release of ^{60}Co from the sediments to the water was important in comparison with radioactive decay, then the model residual sum of squares should be significantly lower using that formulation than the residual sum of squares determined using equation 2. The second method of looking for release of ^{60}Co from the sediments examined the residual variation that was unexplained using equation 2. If remobilization was important, the net rate of removal of ^{60}Co from the water to the sediments should change over time as ^{60}Co accumulates in the lake sediments. We have used both techniques and have not been able to detect a significant release of ^{60}Co from the sediments to the water.

The seasonal simulation model described in the previous section utilized equation 2 to describe the sediment−water−^{60}Co interactions. That model explained 85% of the variation in the measured ^{60}Co concentrations in the water. Substituting equation 3 for equation 2, adjusting T_s in summer and winter, and T_r, and repeating the simulations improved the least squares fit by <1%. The residual sum of squares was not significantly lower than the residual sum of squares calculated using equation 2 ($F = 1.00$, $P < 0.5$). The minimum residual sum of squares occurred with $T_r \simeq \infty$ and T_s values unchanged from earlier results. The residual variation in the model could not be explained by postulating that release of ^{60}Co from the sediments into the water occurred.

In each of the preceding sections, we have examined the residual variation in the ^{60}Co activity measurements for evidence that the rate of transfer of ^{60}Co from the water to the sediments was changing. There was no evidence of any change. Values of T_s derived from the sediment burdens were not statistically different during periods of increasing and decreasing ^{60}Co inputs to the lake. Similarly, there was no systematic temporal trend to the annual fraction of ^{60}Co inputs

retained in the lake sediments. Simulations of the annual average and seasonal ^{60}Co concentrations in the water also provide no evidence that there was a systematic change in the value of T_s. These observations are consistent with the hypothesis that the rate that ^{60}Co was remobilized from the sediments through the water was not significant relative to other processes occurring in the lake. The most significant loss of ^{60}Co from the lake sediments occurs by radioactive decay ($T_{1/2}$ = 5.27 yr).

The lack of significant remobilization of ^{60}Co that we observe is consistent with the behaviour of many other trace metals and their analogs in freshwater sediments. Laboratory experiments (e.g. Alberts and Orlandini 1981), in situ measurements (e.g. Carignan and Nriagu 1985), and simulation models (e.g. Wahlgren et al. 1980; Evans and Dillon 1982) all suggest that under constant environmental conditions, transition metals and their analogs are released slowly, if at all, from lake sediments. There is no evidence that models of ^{60}Co or other elements with similar chemistry need to consider remobilization from the sediments to the overlying water.

Conclusions

Measurements of ^{60}Co activity in Perch Lake have been used to construct a mass balance for the isotope and to examine the transport of ^{60}Co through the lake sediment–water system. Two sets of sediment cores measured 13 yr apart showed very similar ^{60}Co activities. Although the lake sediments contain more than 90% of the activity in the lake at the time the measurements were made, the sediments contained less than 40% of the total decay-corrected ^{60}Co inputs. To account for the accumulated ^{60}Co activity in the sediments, the partial residence time of ^{60}Co in the water was determined to be approximately 1 yr. Simulations of annual ^{60}Co concentrations in the water suggest a shorter residence time of approximately 0.5 yr. Seasonal changes in ^{60}Co concentrations in the water were much larger and more rapid than the long-term trends. Removal of ^{60}Co from the water to the sediments occurred much more rapidly during the summer. During the winter, ^{60}Co concentrations were greater than expected from the addition of new inputs. The simplest explanation for the observed increase is the freeze-out of ^{60}Co from the ice formed during this period. However, the change could also be explained by incomplete mixing of inflowing waters with the lake or by the release of ^{60}Co from the sediments back into the water. ^{60}Co activities in water and in sediments were accurately simulated by a simple, single reservoir model. Partial residence times for removal to the sediments, through the outflow and via radioactive decay, were considered to be constant. There was no evidence that the fractional residence time for removal to the sediments was influenced by the amount of ^{60}Co in the sediments, the rate of ^{60}Co input, or other time-dependent events.

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NOTES

Smolt Transformation and Seaward Migration in 0-Age Progeny of Adult Spring Chinook Salmon (*Oncorhynchus tshawytscha*) Matured Early with Photoperiod Control

W. S. Zaugg

National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest and Alaska Fisheries Center, Coastal Zone and Estuarine Studies Division, 2725 Montlake Boulevard East, Seattle, WA 98112, USA

J. E. Bodle and J. E. Manning

U.S. Fish and Wildlife Service, Little White Salmon National Fish Hatchery, Cook, WA 98605, USA

and E. Wold

National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Environmental and Technical Services Division, 847 N.E. 19th Ave., Suite 350, Portland, OR 97232, USA

Zaugg, W. S., J. E. Bodle, J. E. Manning, and E. Wold. 1986. Smolt transformation and seaward migration in 0-age progeny of adult spring chinook salmon (*Oncorhynchus tshawytscha*) matured early with photoperiod control. Can. J. Fish. Aquat. Sci. 43: 885–888.

Maturation of hatchery-held adult spring-run chinook salmon (*Oncorhynchus tshawytscha*) was accelerated by decreasing photoperiods. Spawning occurred 1 mo earlier than with nontreated fish. Because of early hatching, progeny from the photoperiod regulated adults were larger and exhibited signs of parr–smolt transformation such as changes in coloration and behavior, elevation of gill Na^+-K^+ ATPase activity, and active seaward migration at age 0, nearly 1 yr prior to usual releases of juveniles from normally spawned adults.

En diminuant les photopériodes, on a accéléré la maturation du saumon chinook (*Oncorhynchus tshawytscha*) en bandes printanières, retenu en enclos de pisciculture. Chez ces poissons, le frai a eu lieu un mois plus tôt que chez les poissons non traités. En raison de la rapidité de l'éclosion, le progéniture des adultes à photopériode contrôlée était de plus grande taille et a manifesté des signes évidents de transformation de parr (tacon) en smolt (saumoneau de descente), à savoir des changements de la livrée et du comportement, une augmentation d'activité de la Na^+-K^+ ATPase branchiale, et une migration active en direction de la mer à l'âge 0, presque 1 an avant la libération normale des saumoneaux issus d'adultes produits dans des conditions normales.

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Adult spring-run chinook salmon (*Oncorhynchus tshawytscha*) begin to enter the Columbia River in March as they continue their return journey to native streams and hatcheries, where they generally arrive in April and May. Since spawning does not begin until mid-August, adults must be held at the hatcheries for up to 4 mo. During this time, many die from injuries and disease. Often, holding ponds are lined with sheets of plastic to eliminate injuries from rough surfaces, and returning fish are injected with antibiotics to reduce disease.

At the Little White Salmon National Fish Hatchery (NFH), located on the Little White Salmon River, a tributary of the Columbia River in southwestern Washington, some success in reducing adult mortalities has been achieved by coating concrete holding ponds with a plastic resin and by injecting the returning adults with Erythromycin.[1] More importantly, however, holding time has been reduced by accelerating maturation through photoperiod (day length) control. Spawning times in adults under controlled photoperiod are advanced by about 4 wk. In addition to decreasing adult mortalities by reducing the holding time, another benefit is derived from early spawning, that of increased growth time in progeny as a result of earlier than normal hatching times. Consequently, larger smolts can be produced for releases normally made during their second spring at age 1+ (17–18 mo).

Recently it was noted that progeny from early spawning adults showed physical and behavioral indications of parr–

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1. Comparisons of spawning times, eggs, and progeny information for normal and photoperiod-accelerated maturing spring chinook salmon. Significant differences (ANOVA): $*p < 0.05$; $**p < 0.025$; $***p < 0.005$.

Groups and brood years	Number of females	Spawning dates	Mean egg wt (g) (±SE)	Mean number of eggs per female (±SE)	Mean percent eye-up (±SE)	Mean progeny wt (g) at first feeding, date	Mean progeny wt (g) on 1 October (±SE)
Natural light, 1976–79	5662	11–17 Aug.	0.24 (0.01)**	4175 (324)	84.5 (3.6)	0.32 (0.01)*, 10–28 Dec.	13.8 (0.8)***
Photoperiod accelerated, 1980–82	3884	16–22 July	0.20 (0.01)**	3922 (271)	87.4 (3.2)	0.27 (0.01)*, 29 Oct. – 12 Nov.	24.4 (1.7)***

smolt transformation in their first spring as 0-age fish (about 7 mo), nearly 1 yr prior to scheduled release. These indications have not been observed previously in progeny from normally spawned adults. This communication reports increases in gill Na^+-K^+ ATPase activity and observance of migratory behavior that confirms the visual observations of parr–smolt transformation in 0-age spring chinook salmon juveniles from adults induced to spawn early by photoperiod control. Enzyme determinations on 0-age spring chinook salmon from normally spawned adults at hatcheries similar to the Little White Salmon NFH have shown little or no increases in activity in the first spring.

Methods

Adult spring chinook salmon returning to holding ponds at the Little White Salmon NFH by the second week in May were moved into holding areas covered completely by a metal building (9.9 × 13 m) equipped with six sodium vapor lamps (Lucalox G.E., LU 150/55) located 3.1 m above the water's surface. Beginning about mid-May, adult salmon were exposed to 12 h of light per day, which was then reduced by 30 min per week to about 5 h of light per day at spawning. Fry were reared inside in water ranging from about 7 to 9°C, then in November transferred to outside ponds with water ranging from 4 to 7°C. The fish were fed Oregon Moist Pellets for 15–16 mo until released in the spring of their second year.

Three experimental groups of about 50 000 fish each (1982 brood) were tagged with coded wire tags on 31 March and 1 April 1983. Two groups were released as age 0, one on 4 May and another on 24 June 1983. The third group was released on 19 April 1984 as yearlings with the production fish according to the normal release schedule. On sampling dates, random samples of fish (10–20) were taken by dip net from the experimental groups, weighed, and measured. Gill Na^+-K^+ ATPase activities (micromoles P_i per milligram protein per hour) were determined for individual fish by procedures described in Zaugg (1982a). (Enzyme analyses were also performed on untagged fish released at age 0 in 1982 (1981 accelerated brood) as a preliminary test.) Age 0 migrants were captured in the Columbia River in 1983 by purse and beach seines at Jones Beach, Oregon, 186 km from the release site, weighed, measured, and identified by extracted coded wire tags (Dawley et al. 1985a, 1985b). No ATPase measurements were made on captured migrants. Numbers of migrants were adjusted to reflect a standardized fishing effort.

Results

In 1980, 1981, and 1982, adults subjected to photoperiod control spawned approximately 1 mo earlier than adults in previous years, produced smaller eggs, initially smaller feeding fry, and subsequently larger progeny (Table 1). Gill Na^+-K^+ ATPase activity in 0-age fish increased early in the spring of both 1982 and 1983 and continued to rise until May or June before showing a definite steady decline (Fig. 1). Enzyme activity in 0-age, tagged experimental fish (1983) increased before releases of two groups on 4 May and 24 June (arrows, Fig. 2), and then decreased to a low of 5.2 on 6 January 1984 (not shown). Activities increased again in the spring of 1984 in the age 1+ fish released on 19 April (Fig. 2). During the period of elevated gill Na^+-K^+ ATPase activity in 0-age fish, clearing pectoral and ventral fins and pronounced silvering suggested that parr–smolt transformation had occurred. Mean correlation

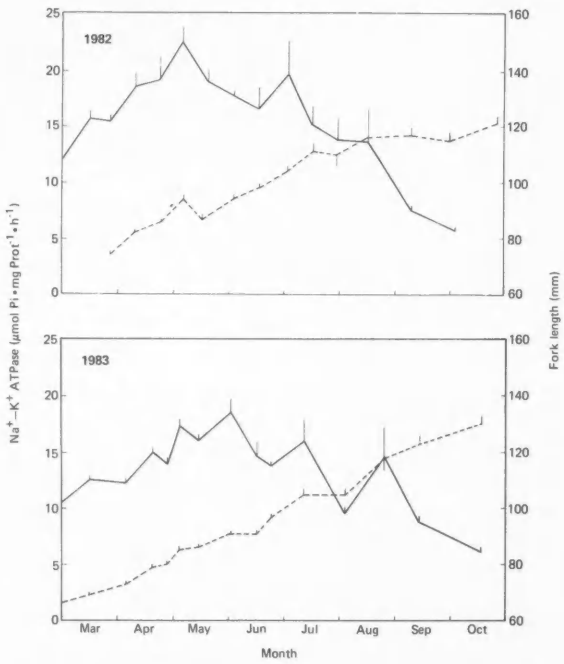

FIG. 1. Gill Na^+-K^+ ATPase activity and fork lengths in 1982 and 1983 0-age spring chinook salmon juveniles from photoperiod-advanced adults. All fish sampled were used for growth curves (---, fork lengths) and for a composite Na^+-K^+ ATPase curve (—) of the three tagged experimental groups in 1983. Standard errors of the mean are identified by vertical lines.

TABLE 2. Length, weight, and migrant information on releases of 0-age smolts.

Experimental information	1983 release date	
	4 May	24 June
Mean wt (g) (± SE) for final Na^+-K^+ ATPase sample (n = 20)	6.2 (0.4)	10.0 (0.3)
Average wt (g) from hatchery release records	6.3	10.3
Calculated mean fork length (FL, mm)[a]		
$y = a + bx$	83[b]	97[c]
$y = ax^b$	84[d]	99[e]
Mean FL at final Na^+-K^+ ATPase sample (± SE)	82 (2)	97 (1)
Mean FL of migrants at Jones Beach (± SE)	89 (1)	111 (1)
Number of tagged fish released	48 145	46 047
Actual (and adjusted) number of migrants captured[f]	42 (43)	44 (90)
Median migration time (days)[g]	16	11

[a] y = FL/wt, x = FL.
[b] a = 46.6, b = −0.40, coefficient of determination r^2 = 0.90.
[c] a = 34.9, b = −0.26, r^2 = 0.86.
[d] a = 152 859, b = −2.11, r^2 = 0.92.
[e] a = 69 452, b = −1.93, r^2 = 0.89.
[f] Adjusted number adjusts for fishing effort (Dawley et al. 1985a, 1985b).
[g] Length of time required for one half of migrants to reach Jones Beach (186 km).

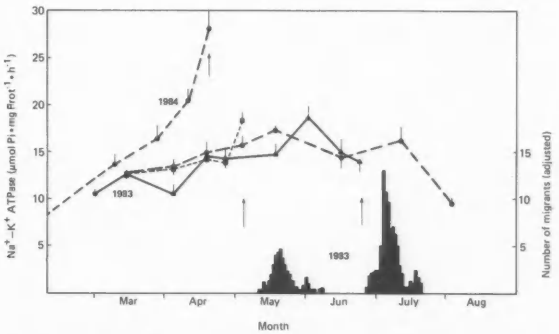

FIG. 2. Gill Na^+-K^+ ATPase activity in 1982 brood release groups of age 0 and age 1+ spring chinook salmon and numbers (adjusted) of migrants captured at Jones Beach. Gill Na^+-K^+ ATPase activities are plotted for each tagged release group (---, 4 May 1983; —, 24 June 1983; −−, 19 April 1984 yearlings); arrows indicate release dates. Histograms show numbers (adjusted) of migrants captured and dates of capture at Jones Beach for each 0-age release group.

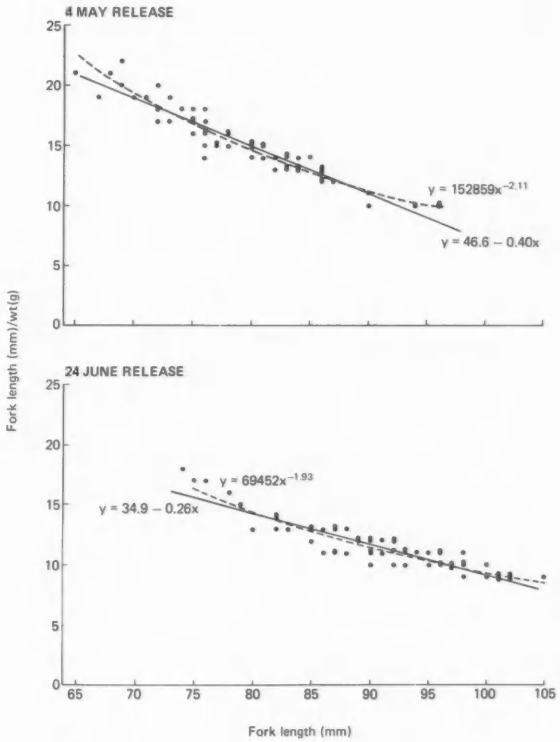

FIG. 3. Relationships between fork length and weight used to calculate mean fork lengths of release groups. Plots of the fork length to weight ratio versus fork length are shown for 0-age fish used in Na^+-K^+ ATPase determinations from 4 April to 3 May 1983 (May release, n = 57) and 17 May to 23 June 1983 (June release, n = 60). Equations derived from these plots were used to calculate the mean fork lengths of released fish from hatchery weight records (See Table 2).

coefficients (r) for the relationship of gill Na^+-K^+ ATPase activity versus fork length for all 0-age fish examined between the first of April and the last of August, the time of changing enzyme activities, were 0.47 in 1982 and 0.42 in 1983.

Since only fish weight was determined at release, mean fork lengths were calculated from relationships between weights and lengths of fish used for Na^+-K^+ ATPase samples (Fig. 3). Mean fork lengths were determined using two different equations (Table 2), both of which gave similar values. Mean fork lengths of migrants captured at Jones Beach were greater than those of release groups at the hatchery (Table 2). Fish released in June migrated more rapidly than those released in May, and when numbers were adjusted for fishing effort, a higher percentage was captured at Jones Beach (Table 2). Eighty-six percent of the fish captured from the 4 May release were taken near shore in the beach seine, whereas all of the fish captured from the 24 June release were taken in the purse seine

at midriver. The numbers of fish captured at Jones Beach reflected typical percentages for 0-age chinook salmon.

Discussion

Photoperiod control dramatically affects reproductive physiology and spawning in salmon and trout (MacQuarrie et al. 1978, 1979; Whitehead et al. 1978a, 1978b; Eriksson and Lundqvist 1980). Subjection of adult spring-run chinook salmon to decreasing photoperiods has resulted in accelerated maturation and earlier spawning times at the Little White Salmon NFH. Although eggs from adults under photoperiod control are smaller than from adults allowed to mature under natural conditions (Table 1), numbers and percent survival to the eyed stage do not differ significantly. Initial feeding begins at a smaller size with early hatching fish and 4–5 wk prior to fish from normal hatchings. Therefore, photoperiod control has reduced adult mortality by decreasing the hatchery holding time and produced larger yearling smolts because of a longer rearing period. However, another important effect of this manipulation appears to be the production of 0-age smolts. The phenomenon of parr–smolt transformation is highly dependent upon age, size, and growth rate (Wagner et al. 1969; Hoar 1976; Ewing et al. 1980). Data reported here on migratory behavior and increased gill Na^+-K^+ ATPase activity suggest that early hatching results in an age, size, growth rate combination that allows parr–smolt transformation to occur in the spring of the first year, nearly 1 yr prior to usual releases of progeny from normally spawned adults at this hatchery. Observations of increased silvering, tail banding, fin clarification, and behavioral changes support this conclusion. Other studies of 0-age spring chinook salmon migrants have been reported, but in these instances fish either experienced more rapid growth because of warmer rearing water (Hart et al. 1981) or showed elevated gill Na^+-K^+ ATPase activity and migration later in the summer and fall seasons of the year (Buckman and Ewing 1982).

Fish released in June migrated more rapidly than those released in May. This is similar to trends of more rapid migration observed in delayed releases of fall chinook and coho (*Oncorhynchus kisutch*) salmon (Zaugg 1981, 1982b). Most migrants from the 4 May release (86%) were captured near shore in the beach seine and only 14% in midriver with the purse seine, whereas all of the fish captured from the 24 June release were taken by the purse seine in midriver. Studies on migratory patterns of 0-age fall chinook salmon (W. S. Zaugg, unpubl. data) indicate that the faster, midriver migrations may be associated with more complete smoltification.

A near linear relationship existed between the ratio of fork length to weight versus fork length for all fish sampled within a month of each release (Fig. 3). This relationship allowed the calculation of mean fork lengths of released groups from weight information, and subsequent comparison with the lengths of migrants reaching Jones Beach (Table 2). The shift toward greater mean lengths in migrants over the released population suggests the loss of smaller fish. Dawley et al. (1985a, 1985b) have reported similar findings in groups of 0-age chinook and yearling coho salmon.

Conclusions as to how successful the controlled photoperiod program is in producing 0-age spring chinook salmon smolts that will survive to contribute to the fishery must await adult returns. However, data showing elevated gill Na^+-K^+ ATPase activity, good movement to the estuary, and recapture of significant numbers of migrants are optimistic observations. Should a 0-age smolt program prove successful, it would become possible to rear three to four times as many smolts at less expense in the same hatchery facilities, a cost-effective means of increasing the resource.

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Optimal Thinning of a Year-Class with Density-Dependent Growth

Rögnvaldur Hannesson

Institute of Fisheries Economics, Norwegian School of Economics and Business Administration, Helleveien 30, N-5035 Bergen-Sandviken, Norway

Hannesson, R. 1986. Optimal thinning of a year-class with density-dependent growth. Can. J. Fish. Aquat. Sci. 43: 889–892.

I consider the impact of density-dependent growth on the optimal harvesting of a year-class of fish. In general, density dependence makes "thinning" of the year-class a desirable strategy. Moderate density dependence implies that thinning should be gradual, even in the case of zero harvesting costs where the optimal harvesting strategy would otherwise be instantaneous harvesting. Strong density dependence calls for an immediate thinning at an early date, in the case of zero harvesting costs.

J'examine les répercussions de la croissance en fonction de la densité sur l'exploitation optimale d'une classe d'âge de poissons. De façon générale, le fait que la croissance dépend de la densité rend souhaitable la réduction de la classe d'âge. Une dépendance modérée envers la densité signifie que la reduction doit être graduelle, même dans le cas de coûts d'exploitation nuls où la stratégie d'exploitation optimale correspondrait par ailleurs à une récolte instantanée. Une dépendance forte envers la densité exige une réduction immédiate à une date avancée, dans le cas où les coûts d'exploitation sont nuls.

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In this note I consider the harvesting of a single year-class of fish with density-dependent growth; i.e. the growth rate of each fish at a point in time depends on how many fish there are in the year-class at that time. One would expect that some "thinning" of the year-class would be desirable in such cases in order to improve the growth of the remaining fish and to enhance the yield of the year-class. This could be accomplished in two different ways: (i) a short harvesting "pulse" followed by a period of uninterrupted growth until the final harvesting phase or (ii) continuous thinning that merges into a final harvesting phase. The purpose of this note is to discuss which of these will prevail. I shall refer to strategy (i) as "instantaneous thinning" and to (ii) as "gradual thinning." This problem does not appear to have been addressed in the literature. This note extends earlier work by Hannesson (1975) and Clark et al. (1973) to cover the case of density-dependent growth.

A Model of Optimal Thinning

Consider the harvesting of a year-class of fish recruited to the fishery at time zero. I define the following variables:

N_t = number of fish at time t
w_t = weight of an individual fish at time t
r = rate of discount
M = instantaneous natural mortality, assumed constant
F_t = instantaneous fishing mortality at time t
c = cost per unit F, assumed constant

$$\dot{N}_t = \frac{dN}{dt} = -(F_t + M)N_t$$

$$\dot{w}_t = \frac{dw}{dt} = g(t, N_t).$$

The argument N_t in $g(\cdot)$ reflects density dependence in the growth of individual fish. Using subscripts to denote partial derivatives of g, we assume that $g_N \leq 0$, with equality implying the absence of density dependence.

Here, I shall ignore problems raised by the price of fish varying with time, the age of fish, or quantity harvested. For simplicity I put the price of fish equal to 1, expressing all values in units of fish as it were. Maximizing the present value of harvesting the year-class then defines the following problem:

$$(1) \quad \max_{F_t} \int_0^\infty F_t(N_t w_t - c)\, e^{-rt}\, dt$$

subject to

$$(2) \quad \dot{w}_t = g(t, N_t)$$

$$(3) \quad \dot{N}_t = -(F_t + M)N_t$$

$$(4) \quad 0 \leq F_t \leq F_{\max}.$$

Problems of this kind may be solved by applying the maximum principle (cf., e.g., Clark 1976, Chap. 4). This involves maximizing the so-called Hamiltonian function, $H(\cdot)$, which consists of the integrand in (1), plus the side constraints (2) and (3) multiplied by adjoint dynamic variables. The present value of the Hamiltonian for this problem is

$$(5) \quad H_t = [F_t(N_t w_t - c) + \lambda_t g(t, N_t) - \gamma_t(F_t + M)N_t]\, e^{-rt}$$

where λ_t and γ_t denote the adjoint variables corresponding to the state variables w_t and N_t, respectively. For a similar treatment, in terms of maximizing the harvested biomass, see Goh (1980, p. 147–158).

According to the maximum principle, the evolution of the adjoint variables is determined as follows (subscripts denote here partial derivatives, and I henceforth drop the time subscripts wherever this causes no confusion):

(6) $\dot{\gamma} = \gamma(r + M) - \lambda g_N + F(\gamma - w)$

(7) $\dot{\lambda} = r\lambda - FN.$

Taking the derivative of H_t with respect to the control variable F_t defines the optimal control of F as follows:

(8a) $F = 0$ when $N(w - \gamma) < c$

(8b) $0 \leq F \leq F_{\max}$ when $N(w - \gamma) = c$

(8c) $F = F_{\max}$ when $N(w - \gamma) > c.$

The adjoint variable γ may be interpreted as the value foregone by harvesting a fish at time t instead of leaving it to grow further and to be harvested at a later date. Equation (8a) says, then, that no harvesting should take place when the value of fish landed, including the future value foregone, is less than the cost of harvesting. Equations (8b) and (8c) state the opposite, the difference between them being that the instantaneous rate of harvesting is indeterminate when the value of fish landed is equal to the harvesting cost. Otherwise, harvesting should take place at maximum capacity.

On the basis of (8) we may distinguish between two harvesting strategies. (i) Equation (8b) holds only at a point in time, so that either $F = 0$ or $F = F_{\max}$ until the desired harvest has been taken. Assuming that $F_{\max}$ is "large," this is referred to as "instantaneous harvesting." (ii) Equation (8b) holds for a period of time during which $0 < F < F_{\max}$, its optimal value being determined by the optimal evolution of the year-class biomass (Nw). I shall refer to this as "gradual harvesting."

Consider now the case where (8b) holds for a period of time. Differentiating (8b) with respect to time, solving for $\dot{\gamma}$, and setting equal to (6) yields

(9) $Nw(r + M - g/w - \lambda g_N/w) = rc.$

When r and M are constant, $rc = 0$ and $g_N = 0$, and g/w is a monotonically decreasing function of time, (9) can only be satisfied at a point in time. Hence, instantaneous harvesting at that time will be the optimal strategy. With density-dependent growth ($g_N < 0$), it is possible that the term in parentheses in (9) will be zero over an interval, as thinning the population will raise g and so compensate for the otherwise falling rate of growth (g/w). It is thus possible that density-dependent growth will make gradual harvesting preferable to instantaneous harvesting even if $rc = 0$. The optimal thinning strategy need not, therefore, be instantaneous thinning, even if instantaneous harvesting would be the optimal strategy in the absence of density-dependent growth.

When $rc > 0$, division by the term in parentheses in (9) gives

(10) $Nw = rc/(r + M - g/w - \lambda g_N/w).$

Setting this equal to Nw, as determined by (2) and (3) and the initial values N_0 and w_0, defines the optimal control of the biomass (cf. Hannesson 1975). For "small" t the right-hand side of (10) is negative, (8a) holds, and $F = 0$. At some time t^* a discontinuity occurs in (10) as the numerator of the right-hand side becomes zero. At $t^{**} > t^*$, (10) will attain the same value as the unharvested year-class biomass (Nw determined by (2) and (3) with $F = 0$) and harvesting begins. Harvesting will end at t^{***} when $Nw = c$ and $M = g/w$, as extending the harvesting beyond t^{***} would yield a negative contribution to the objective function (1). Density dependence ($g_N < 0$) moves the harvesting period forward in time, with the discontinuity in (10) occurring earlier and displacing t^* and t^{**} to the "left" on the time axis.

An interesting interpretation of (9) may be obtained by solving for λ. From (7) we get

(11) $\lambda_t = e^{rt} \int_t^\infty F_S N_S e^{-rs}\, dS.$

Thus, λ_t expresses the present value at time t of the *number of fish* that from then on will be harvested from the year-class. Next, note that (9) implies

(12) $[g - Mw]\Delta t = [r(w - c/N) - \lambda g_N]\Delta t.$

The bracketed term on the left-hand side of (12) shows the expected growth of a fish left unharvested (gross growth less natural mortality rate multiplied by the weight of the fish). The left-hand side of (12) may therefore be interpreted as the expected return from leaving a fish unharvested for a "short" period Δt. The term $r(w - c/N)\Delta t$ expresses the rate of return from investing the value of a harvested fish (i.e. its weight less the harvesting cost per fish, cF/FN). The term λg_N reflects the additional return a harvested fish will yield if growth is density dependent; g_N shows the increase in the growth of each fish if "one fish" is removed from the year-class, and multiplication by λ gives the resulting increase in the present value of the catch (the present value of the number of fish whose growth has been improved and that will be caught). Equation (12) thus says that the year-class biomass should be so controlled that "the law of indifference" holds between harvesting one more fish now and leaving it in the sea. Normally the weight of each fish will be so low initially that (12) cannot be satisfied, the rate of return on unharvested fish being higher than that of a harvested fish, even without any thinning of the year- class. As the fish grow and the relative growth rate (g/w) falls, (12) will sooner or later be satisfied, and the thinning/harvesting process begins.

An Example

In this section I shall use a version of the logistic growth function to illustrate and further examine the theoretical results obtained in the preceding section. I have chosen this function because it is relatively simple to manipulate and appears capable of representing density-dependent growth in a reasonable manner. In applied work, other forms may indeed be more adequate.

In the preceding section it was found that the optimal thinning of a year-class might be gradual, even if the optimal strategy in the absence of density-dependent growth is one of instantaneous harvesting ($cr = 0$). Here, I shall present numerical examples confirming this. There are, however, other cases in which it is possible to satisfy equation (9) over a period of time, but where instantaneous thinning nevertheless is the best strategy.

The logistic function is derived from the parabolic function

(13) $\dot{w}_t = aw_t - bw_t^2,$

which upon integration yields

(14) $$w_t = \frac{a/b}{1 + \left[\frac{a/b - w_0}{w_0}\right] e^{-at}}.$$

Substitution of (14) into (13) gives $\dot{w}_t = g(t)$.

Suppose that the number of fish in the year-class affects the coefficient a. This would be consistent with interpreting the first term on the right-hand side of (13) as representing the

intake of food, with the ability to acquire food growing proportionally with body weight and the availability of food being reflected by a. A simple way of modelling density dependence of a is the following:

$$(15)\quad a = a_0 - \alpha(N_t/\bar{N}_t)^{\beta}$$

where a_0, α, and β are parameters and $\bar{N}_t$ is the number of fish surviving at time t in the absence of harvesting. This implies that thinning the population will always improve growth, no matter at which age it is applied. In reality, growth is more likely to be density dependent when the year-class is young and numerous, so that thinning at a late stage in the life of year-class will be less likely to produce an improvement in growth.

Substitution of (13) and (15) into (9) gives

$$(16)\quad N_t w_t \phi(t) = rc$$

where

$$(17)\quad \phi(t) = r + M - a_0 + \alpha(N_t/\bar{N}_t)^{\beta} + bw_t + \alpha\beta N_t^{\beta-1}\bar{N}_t^{-\beta}\lambda_t.$$

Consider first the case $r = 0$, $c = 0$. Suppose $\phi(0) < 0$. Hence, $F_0 = 0$. Since $\dot{\phi} > 0$ for $F = 0$, $\phi(t) = 0$ for some $t > 0$. Differentiating $\phi(t)$ with respect to time and setting $\dot{\phi}(t) = 0$ gives (note that $N_t/\bar{N}_t = \exp[-\int_0^t F_S dS]$):

$$(18)\quad F_t\alpha\beta[2 + (\beta - 1)\dot{\lambda_t}/N_t]\exp\left(-\beta\int_0^t F_S dS\right) = b\dot{w}_t + \alpha\beta M N_t^{-1}\lambda_t \exp\left(-\beta\int_0^t F_S dS\right).$$

Since the right-hand side of (18) is always positive and $\lambda_t < N_t$ (cf. 11), it is always possible to find some $0 < F < \infty$ satisfying (18), which means that once $\phi(t) = 0$ and harvesting begins, it is possible to apply gradual harvesting such that $\phi(t)$ will remain zero for a period of time. In the cases to be presented below, I have calculated the optimum harvesting pattern implied by $\phi(t) = 0$ as follows. For a given a_t the value of F giving $\phi(t + \Delta t) = 0$ was calculated, and then $a_{t+\Delta t}$ was adjusted according to (15) and the process repeated. These calculations were repeated for various initial values of λ until the one was found which gave $\lambda_{\bar{t}} = \int_{\bar{t}}^{T} F_S N_S dS$, $\bar{t}$ being the time at which the harvest begins and T the time when some insignificant fraction was left of the number of fish recruited at $t = 0$.

Figure 1 shows the evolution of the year-class biomass in the absence of harvesting, together with optimal gradual harvesting with density dependence. Since $r = 0$ and $c = 0$, instantaneous harvesting at $t = 6.16$ would be the optimal strategy in the absence of density-dependent growth. The three cases of density dependence shown in Fig. 1 refer to $\beta = 0.1$, $\beta = 1$, and $\beta = 2$, respectively, while $\alpha = 0.4$ in all cases. Other parameters were set as follows: $w_0 = 0.47426$, $a_0 = 1$, $b = 0.06$, so that $a = 0.6$ in the absence of density dependence. Figure 2 shows how the coefficient a varies with the ratio of the harvested population to the unharvested one ($N_t/\bar{N}_t$). The benefits of thinning the population are seen to be more rapidly acquired the larger β is. From Fig. 1 we see that the thinning process begins earlier and is more gradual the larger β is.

The fact that it is *possible* to satisfy (9) and (16) over a period of time is not sufficient, however, to establish that gradual thinning is the optimal strategy. In order to investigate the optimality of the gradual harvesting shown in Fig. 1, it may

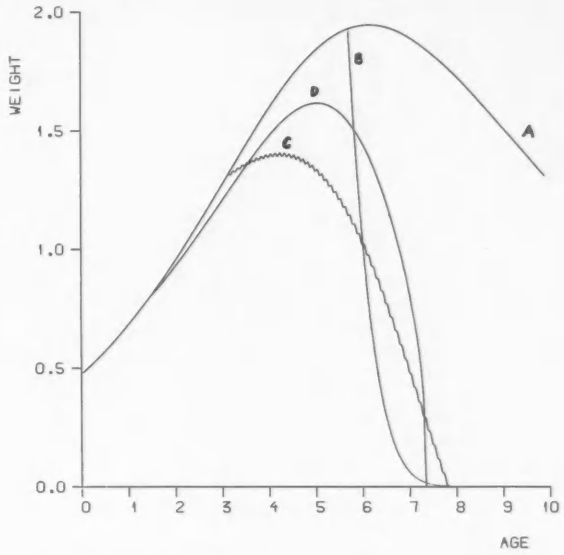

FIG. 1. Optimal harvesting of biomass with density-dependent growth. Curve A: evolution of biomass in the absence of harvesting; curve B: harvesting with $\beta = 0.1$; curve C: harvesting with $\beta = 1$; curve D: harvesting with $\beta = 2$.

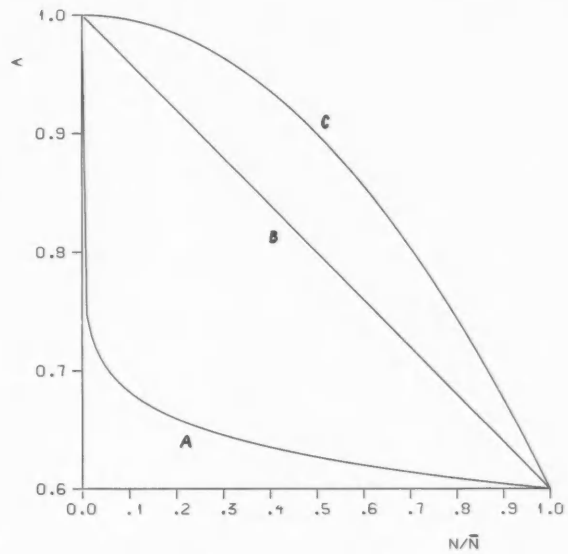

FIG. 2. How the coefficient a varies with $N/\bar{N}$ when β equals 0.1 (curve A), 1 (curve B), and 2 (curve C).

be compared with the best possible instantaneous thinning strategy. The latter is defined as follows. At time t_1 a fraction δ of the population is harvested. Thereafter the population is left to grow until it has attained its maximum biomass at time t_2, determined by $\dot{w}_t/w_t = r + M$. At t_2 the remaining population is harvested. The optimal strategy is the one which solves the following problem:

$$(19)\quad \underset{t_1,\delta}{\text{Max}}\ [\delta\bar{N}_{t_1}w_{t_1} + (1 - \delta)\bar{N}_{t_2}w_{t_2}]$$

TABLE 1. Comparison of instantaneous and gradual harvesting strategies. Total catch ($N_0 = 1$, $\alpha = 0.4$, $M = 0.2$, $a_0 = 1.0$, $b = 0.06$, $w_0 = 0.47426$).

	Extended harvesting	Two-phased instantaneous harvesting
$\beta = 2$	2.517	2.495 ($t_1 = 0$; $t_2 = 5.5$; $\delta = 0.69$)
$\beta = 1$	2.222	2.150 ($t_1 = 4.8$; $t_2 = 6.9$; $\delta = 0.53$)
$\beta = 0.1$	1.958	1.953 ($t_1 = 5.7$; $t_2 = 6.4$; $\delta = 0.5$)

in the case where $r = 0$ and $c = 0$.

In Table 1 the gradual thinning strategy is compared with the strategy resulting from maximizing (19). In all three cases shown, gradual thinning yields a larger catch. The difference is small, however, in the case $\beta = 2$ and $\beta = 0.1$, albeit for very different reasons. When β is close to zero, a significant improvement in growth requires harvesting a very large proportion of the year-class. To do so at an early age would eliminate most of the fish before they had utilized their growth potential. Thinning is then undesirable until shortly before the year-class reaches its maximum biomass, which leaves little time to reap the benefits of the improved growth conditions. When $\beta = 2$ a substantial improvement in growth would result from only a slight thinning of the population. When following the gradual thinning strategy the benefits of thinning are small initially but increase over time. An instantaneous thinning at an early date would lead to an immediate improvement in the growth conditions and leave more time for reaping the benefits thereof. Since in this case only moderate thinning is required to obtain a substantial improvement in growth, instantaneous thinning need not be much inferior to gradual thinning.

The fact that the search for the best instantaneous thinning strategy led to an immediate thinning at $t = 0$ when $\beta = 2$ leads one to suspect that this strategy might in fact be the optimal one in this case, if it were possible to apply it before that date. This is indeed so. Lowering the age of recruitment renders instantaneous thinning superior to gradual thinning. For example, with the age of recruitment set at $t = -5$, gradual thinning yields a total catch of 2.524, while instantaneous thinning yields a total catch of 3.099 (with $t_1 = -5$, $t_2 = 3.96$, and $\delta = 0.64$). Raising the value of β (e.g. to $\beta = 3$) also makes instantaneous thinning preferable to gradual thinning without lowering the time of recruitment.

Finally, consider the case $r > 0$ and $c > 0$. Substitution of (13) and (15) into (10) gives

$$N_t w_t = rc/\phi(t). \quad (18)$$

Figure 3 shows the optimal control of the biomass according to (18) during the harvesting phase ($c = 0.5$, $r = 0.1$, and $\beta = 2$ in the density-dependent case). Maximum potential biomass of the year-class would be obtained at $t = 6.16$, but harvesting in the absence of density-dependent growth begins at $t = 5.3$. Density-dependent growth is seen to prolong the harvesting phase, with thinning starting already at $t = 1.8$. The resulting rise in the growth coefficient raises the relative growth rate for any given w and postpones the date at which the expected growth of an unharvested fish becomes zero (i.e. when $g - Mw = 0$) and harvesting ends.

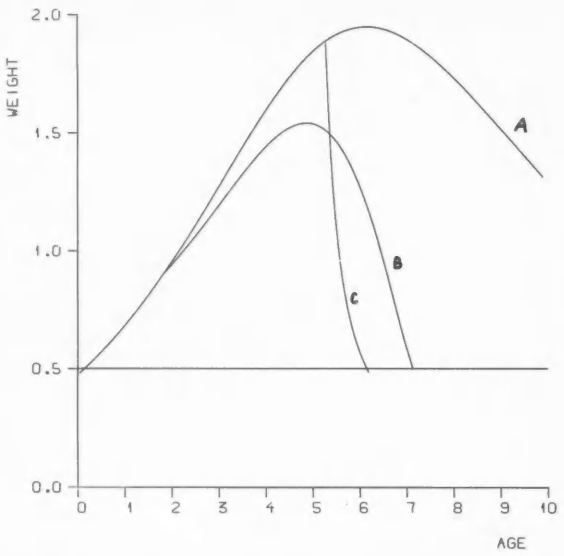

FIG. 3. Evolution of biomass in the absence of harvesting (curve A) and with optimal harvesting with (curve B) and without (curve C) density-dependent growth, when $c = 0.5$ and $r = 0.1$.

Conclusion

In this note we have studied how density-dependent growth of fish affects the optimal harvesting of a year-class. Not surprisingly, we have found that such dependence advances the date at which harvesting begins, as thinning the population improves the growth potential of the remaining fish. What is less obvious is that the thinning process should in certain cases be a gradual process instead of instantaneous. In particular, it is possible that the optimal thinning is gradual and not instantaneous, even if instantaneous harvesting would be the optimal strategy in the absence of density-dependent growth. This is clearly illustrated by the zero cost case, in which gradual thinning is optimal in certain cases, whereas instantaneous harvesting is always optimal in the absence of density-dependent growth. In the zero cost case, gradual thinning is most likely to be the optimal strategy for moderately density-dependent growth, while strongly density-dependent growth calls for a substantial thinning of the year-class at an earlier possible date. The presence of harvesting costs makes it more likely that gradual thinning is the optimal strategy, just as the optimal harvesting period is prolonged by increasing harvesting costs in the case of no density dependence.

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Source of Error in Water Velocity Measurement for Aquatic Studies

D. L. Morantz, S. E. Barbour, and R. K. Sweeney

Department of Fisheries and Oceans, P.O. Box 550, Halifax, N.S. B3J 2S7

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Water velocity is an important component in aquatic studies but is subject to alteration by the presence of an underwater observer. Tests using two types of water velocity meter and a snorkeler showed the effects to be a function of the diver's distance from the probe. Lateral positions generally caused an acceleration of flow at the measurement point of up to 150%, while downstream positions resulted in a decrease in flow of up to 65%. It is recommended that where underwater observers are employed, they position instruments that can be read remotely and then move well away from the point of measurement.

La vitesse de l'eau est un paramètre important dans les études aquatiques, mais elle peut être perturbée par la présence d'un observateur sous l'eau. Des expériences utilisant deux types de compteur de vitesse de l'eau en présence d'un plongeur ont montré que les effets étaient fonction de la distance entre la sonde et le plongeur. La présence d'un observateur d'un côté ou de l'autre de la sonde entraîne généralement au point de mesure une accélération du débit atteignant jusqu'à 150 %, tandis que lorsque l'observateur se poste en aval, il y a une diminution du débit atteignant 65 %. Il est recommandé qu'en présence d'observateurs sous l'eau, ceux-ci placent leurs instruments de manière qu'ils puissent être lus à distance, puis se déplacent loin du lieu des mesures.

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Water velocities are commonly measured in aquatic ecology, since they define, in part, the physical microhabitats used by organisms in streams. For instance, water velocity appears to be the physical characteristic predominantly influencing the positions occupied by some fish (Everest and Chapman 1972; Symons and Heland 1978; Shirvell and Dungey 1983; Rimmer et al. 1984). Because of the extinction of water velocities with depth over a gravel–cobble substrate (Leopold et al. 1964), accurate measurements of focal or nose position velocities are possible only if the current speed meter is positioned by a snorkeler or diver who has carefully observed and marked the site occupied by a fish.

The purpose of this study was to determine whether an underwater observer in proximity to a current meter would significantly alter the water velocity at the position of the fish. For example, the midget Bentzel current speed tube (Everest 1967) must be held in position by a diver, since this instrument is usually employed wholly submerged, while an Ott meter can be positioned by a diver who can then move away during the measurement. The comparability of velocity data among studies could be thrown into question if measurement techniques inadvertently affect measured velocities.

Materials and Methods

We determined the influence of an underwater observer on water velocities by positioning a snorkeler at variable distances from current speed measurement instruments in two streams in Nova Scotia. An Ott current meter fitted with a 3.0-cm propeller and a midget Bentzel current speed tube (Everest 1967) modified as described by Rimmer et al. (1984) (having a flowmeter with an inside diameter of 1.59 mm) were used during these tests.

The accuracy of the Ott meter was tested by calibrating it against a second, identical Ott meter and a Marsh McBirney model 511 electromagnetic current meter in a portable flume. Measurements by these meters were not significantly different (t-tests, $P > 0.05$, $N = 9$) in water velocities ranging from 0.06 to 0.66 $m \cdot s^{-1}$. The midget Bentzel current speed tube was then calibrated against the Ott meter in the portable flume. The linear regression of the Bentzel tube flowmeter measurement against water velocity was highly significant ($R^2 = 0.93$, $P < 0.01$, $N = 15$).

Test 1 — The first test, to measure the effect of a diver near a current meter, was conducted in a 10-m-wide stream with a predominantly cobble–boulder substrate. At four sites a snorkeler consecutively positioned the current speed instruments 2 cm from the substrate. Water velocity measurements were then taken with the underwater observer lying 10–20 cm (measured from the meter to the crown of the snorkeler's head) from each instrument in the three, six, and nine o'clock positions (12 o'clock points upstream). Water velocities were also recorded using the Ott meter while the snorkeler was absent. This was not done using the Bentzell tube because it could only be read underwater. It was noted at all sites that the nine o'clock side of the river contributed the greater proportion of flow.

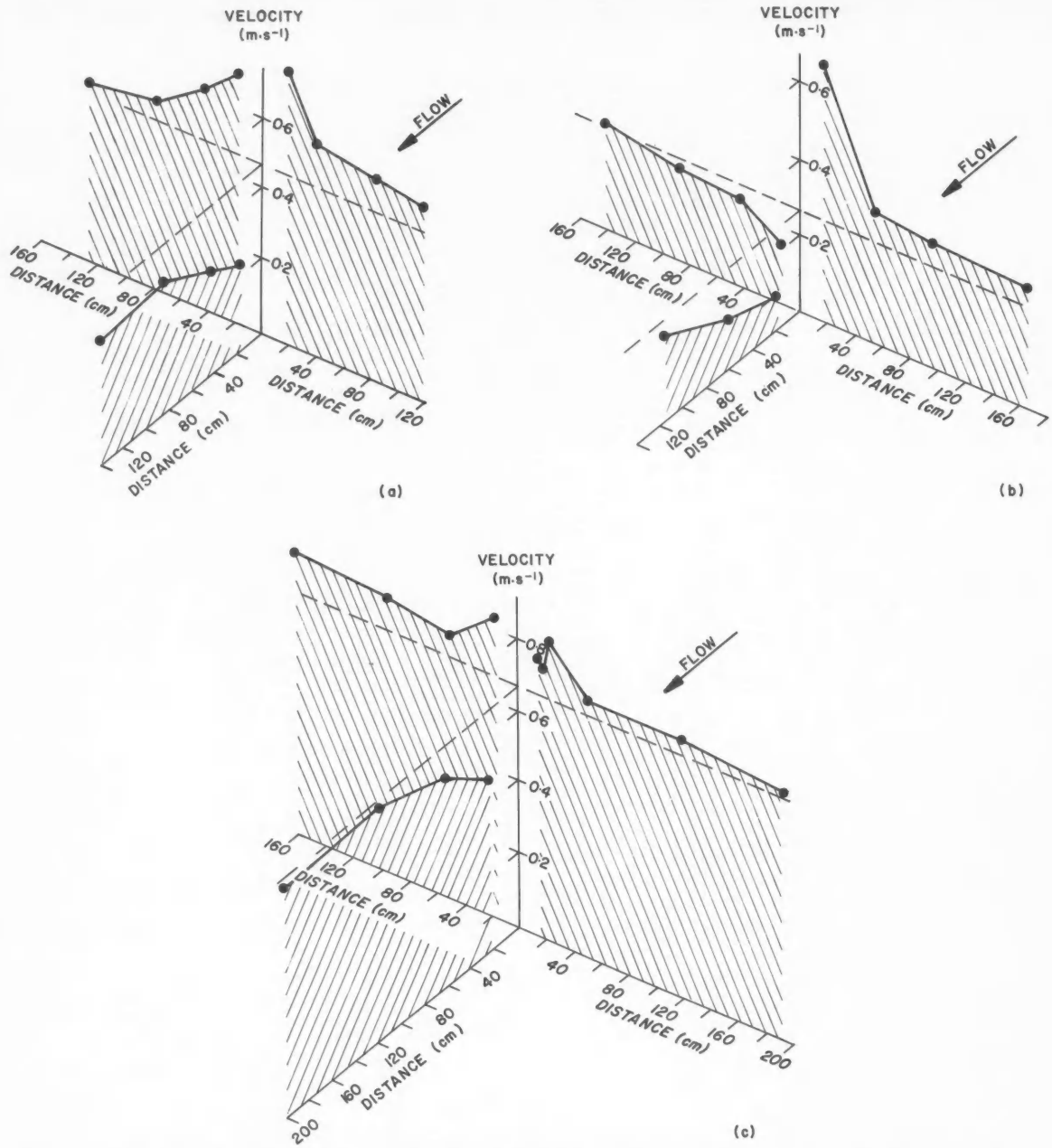

FIG. 1. Effect on water velocity of a diver at various distances radiating from three measurement sites (a, b, c). The broken line represents water velocity in the absence of the diver.

Test 2 — This test, conducted in a 15-m-wide, gravel bottom river, was designed to determine the influence on measured velocities of an underwater observer positioned at variable distances from the current meter. In each of the three, six, and nine o'clock positions (12 o'clock points upstream) at three sites, water velocities were recorded with the snorkeler lying at measured distances (Fig. 1) from the Ott meter (the horizontal distance from the propeller to the crown of the snorkeler's head). The snorkeler then left the water and the measurement was repeated. The meter wading rod was held by an individual standing downstream, at arm's length and to the side.

A test of whether an observer standing near the Ott meter wading rod influenced water velocities was conducted by making five measurements with the observer absent (standing on an emergent boulder) followed by five measurements with the observer present (standing at arm's length, downstream

TABLE 1. Comparisons of stream water velocities recorded by two current measurement instruments with a snorkeler at various positions around each meter.

Site	Snorkeler position (o'clock)[a]	Ott meter		Bentzel tube[b]	
		Velocity ($m \cdot s^{-1}$)	Percent difference	Velocity ($m \cdot s^{-1}$)	Percent difference[c]
1	3	0.27	39	0.34	23
	6	0.36	18	0.32	27
	9	0.63	43	>0.57	>30
	Diver absent	0.44±0.01			
2	3	0.45	45	0.13	58
	6	0.13	58	<0.12	>61
	9	0.51	65	0.12	61
	Diver absent	0.31±0.0			
3	3	0.08	0	<0.12	>50
	6	0.08	0	<0.12	>50
	9	0.07	13	<0.12	>50
	Diver absent	0.08±0.01			
4	3	0.82	27	0.57	49
	6	0.89	21	0.57	49
	9	1.25	12	>0.57	>49
	Diver absent	1.12±0.01			

[a]"Diver absent" position velocities for the Ott meter are mean values from three measurements (±SD).

[b]0.12 and 0.57 $m \cdot s^{-1}$ are, respectively, the lowest and highest velocities which could be measured by the Bentzel tube used.

[c]Calculated as (velocity measurement with diver in water)/(Ott meter velocity measurement with diver absent) × 100.

and to the side of the Ott meter wading rod) at each of two locations.

Results and Discussion

Test 1 — Water velocities measured with the snorkeler near the Ott meter were significantly different from those measured when the snorkeler moved away, at sites 1, 2, and 4 (*t*-test, single specimen compared with a sample (Sokal and Rohlf 1969), $P < 0.02$ in all cases (Table 1)). Water velocities did not vary significantly in site 3. There, flow was sluggish near the stream bottom due to the proximity of boulders both upstream and downstream. It is probable that these boulders negated any effects on velocity caused by the snorkeler.

Velocities were almost always depressed when the snorkeler was located in the six o'clock position (downstream of the current meter). Conversely, water velocities were uniformly highest with the observer lying at nine o'clock to the meter.

Water velocities measured by the midget Bentzel current speed tube also varied because of snorkeler position (Table 1). In two of the three cases where velocities were detectable by this instrument, values were highest (the indicator ball reached the top of the tube) with the snorkeler lying in the nine o'clock position. Measurement errors were inevitable with this instrument, since it was designed to be read from the three o'clock side only. The snorkeler was forced to peer around or over the tube from the other two positions, thereby altering current flow around the instrument. Only velocities between 0.12 and 0.57 $m \cdot s^{-1}$ were measurable with the Bentzel tube used.

Test 2 — Water velocities changed significantly (*t*-test, $P < 0.02$ in all cases) as the snorkeler approached within 0.5 m of the Ott meter position from any direction (Fig. 1). In the lateral positions, the maximum deviation from the velocity measured with the snorkler absent was +148% (at 13 cm from the probe in the three o'clock position, Fig. 1b). From the downstream position, the maximum difference of −67% was recorded with the observer positioned 20 cm from the meter (Fig. 1b). Photographs show that water was dammed upstream of the snorkeler's body in the three and nine o'clock positions and was then funnelled around his head directly into the meter. This was particularly evident on the higher flow side (the three o'clock position) of this river. The damming was not detected in the nine o'clock position in site 2 (Fig. 1b), a nearshore site where flow was quite low. Water was consistently dammed upstream of the snorkeler when he was positioned at six o'clock causing backpressure and reduced water velocities at the meter.

We found that there was no effect from the observer standing at arm's length to the wading rod ($t = 1.8$, $P = 0.11$ and $t = 1.3$, $P = 0.22$ at each of the two sampled sites, respectively).

Water velocity is a common measurement in lotic ecological investigations and in hydrology and river engineering studies. It is therefore important that water velocity data be accurately collected for comparability among studies in diverse locations. We have shown, however, that measurement techniques may significantly influence water velocity data.

The underwater proximity of an observer or equipment to a flow meter can result in erroneous velocity measurements. During microhabitat investigations, we therefore recommend that after appropriate positioning of mechanical or electromagnetic current meters, snorkelers or divers move a minimum of 1.5 m downstream of the instrument. Further, individuals holding the meter wading rods should stand downstream and to the side and as far as possible from the meter.

Instruments such as the midget Bentzel current speed tube must be read by an individual positioned underwater. For this reason the water velocities reported by investigators who have employed these tubes (Everest and Chapman 1972; Symons and Heland 1978; Fausch and White 1981; Rimmer et al. 1984) may be in error. We cannot suggest a factor to correct such errors, since their direction and magnitude are dependent on site-specific flow conditions (Table 1).

The midget Bentzel tube was modified from a larger instrument originally described by Welch (1948). This 1.3-m-long device could be mounted on a wading rod and positioned similarly to a mechanical meter. In this way, it would be possible to benefit from this instrument's advantages (Everest 1967) without prejudicing the results.

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Capture–Recapture Experiment with Fly-Caught Brown (*Salmo trutta*) and Rainbow Trout (*S. gairdneri*)

L. D. Favro and P. K. Kuo

Department of Physics, Wayne State University, Detroit, MI 48202, USA

and J. F. McDonald

Department of Mathematics, University of Windsor, Windsor, Ont. N9B 3P4

Favro, L. D., P. K. Kuo, and J. F. McDonald. 1986. Capture–recapture experiment with fly-caught brown (*Salmo trutta*) and rainbow trout (*S. gairdneri*). Can. J. Fish. Aquat. Sci. 43: 896–899.

A data base on angler-captured brown (*Salmo trutta*) and rainbow trout (*S. gairdneri*) in the Au Sable River of Michigan is analyzed and compared with electrofishing data. The angling recapture frequency for brown trout increases rapidly with increasing length, while the recapture frequency for rainbow trout is independent of length. Anglers caught a greater number of fish over 33 cm long than did the electrofishers in the same water. The anglers and the electrofishers appear to have captured fish from different subpopulations; therefore, conclusions based on data obtained by one capture method may not be applicable to the other.

On analyse une base de données sur les truites brunes (*Salmo trutta*) et arc-en-ciel (*S. gairdneri*) capturées par des pêcheurs à la ligne dans la rivière Au Sable, au Michigan, et on la compare aux données obtenues avec la pêche électrique. La fréquence des recaptures de truites brunes par la pêche à la ligne augmente rapidement avec la longueur tandis que la fréquence des recaptures de truites arc-en-ciel est indépendante de la longueur. Les pêcheurs à la ligne ont capturé un plus grand nombre de poissons mesurant plus de 33 cm que ne l'ont fait les pêcheurs à l'électricité dans les mêmes eaux. Les pêcheurs à la ligne et les pêcheurs à l'électricité semblent avoir capturé des poissons provenant de différentes sous-populations; par conséquent, les conclusions basées sur les données obtenues avec une méthode de capture pourraient ne pas être applicables à l'autre.

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This note analyzes and interprets an extensive data base on angler-captured brown (*Salmo trutta*) and rainbow trout (*S. gairdneri*). It was established by intensive fly fishing of one short section of the Au Sable River of Michigan by three anglers (L. D. Favro, E. J. McGlinn, and S. M. Powell) over a period of more than 10 yr. All trout over 30 cm long plus a significant fraction of those between 25 and 30 cm were tagged with numbered tags and released.

Study Site

This experiment was conducted on a stretch of the Mainstream of the Au Sable River near Grayling, Michigan, between Whirlpool and Thendara roads. This stretch is approximately 1.5 km in length, and is part of the much longer (13.9 km) stretch which has for decades been restricted to fly fishing only. In this section, the river ranges from 10 to 25 m in width and the average central speed of the water is approximately 3 km/h. The central depth typically ranges from 0.5 m to about 1.0 m with five or six deeper holes scattered along its length.

The Au Sable, like most Michigan streams, has a bottom which is mostly sand and gravel. Principal obstructions to the current are a multitude of fallen streamside trees with their associated collections of brush and debris. The water is normally quite clear.

Methods

The fish in this experiment were captured almost exclusively by what can be described as "dry fly fishing" (i.e. the lures were cast with conventional fly tackle and were on the surface). As is common on Michigan streams, the flies were often in hook sizes of fours, sixes, or eights and most of the fishing was done after dark. Fish that exceeded a nominal length of 30.5 cm

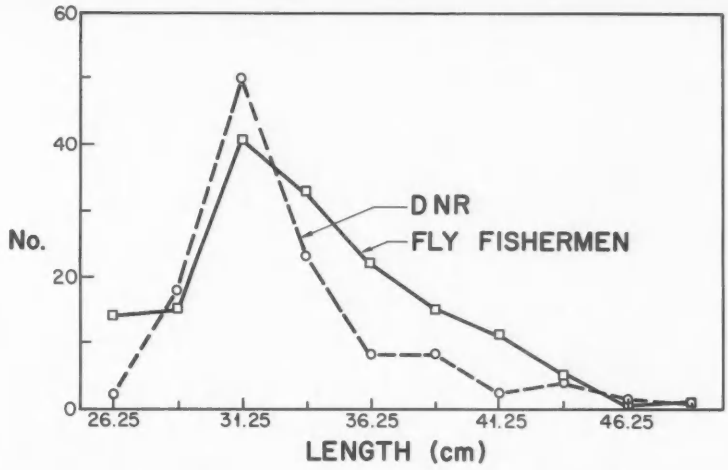

FIG. 1. Size distributions for brown trout (*Salmo trutta*). The curve labelled "fly fishermen" is the distribution for fish caught by the anglers in 1973. The curve labelled "DNR" is the distribution for fish caught by the Michigan Department of Natural Resources using electrofishing in 1973.

were tagged and released. The tags used were No. 10 monel metal bands manufactured by the National Band and Tag Co. of Newport, Kentucky. These were clamped around the side of the lower mandiable. Fish were netted in a reasonably short time after hooking and then dumped onto whatever surface was available, handled with wet or dry hands as the case might be, and forcibly subdued for measuring and tagging. Although an attempt was made to measure the overall length of the fish in a straight line to an accuracy of plus or minus 0.5 cm, the conditions under which the measurements were made (darkness, unanethetized fish, etc.) undoubtedly contributed some small additional error.

The date and location of each capture as well as the tag number and length of each fish at the time of capture were recorded. Locations were identified both by reference to numbered subsections (approximately 100 m in length) used by the Michigan Department of Natural Resources (DNR) and by local landmarks. In the original written records the locations are accurate to approximately 2 m. In the computer file derived from those records, they are identified by the DNR's subsection numbers and decimal fractions thereof. Lengths of the fish ranged from 25 to 53 cm and the total number of captures (including recaptures) was 860.

The experiment began in 1973 and has continued to the present. Data on *initial* captures reported here cover only the period from 1973 to 1976 inclusive. The data do include *recaptures* of fish in 1977 and later years if those fish were initially captured in the previous period.

Unfortunately, the angler's records do not include information about the hours fished each day or even which days were fished if no fish were captured. However, during the 1973–76 period, at least one of the participants was on the stream for half of the fishing season.

In addition to the angling data described above, in 1973, just prior to the opening of the fishing season in late April, the DNR provided 116 electrofishing taggings using the same type of tag in the same section of the river. This was part of a larger electrofishing effort that consisted of shocking a 5.9-km stretch and tagging all fish over about 30 cm.

Results

For purposes of analysis the fish were grouped by length into 2.5-cm-wide intervals starting at 25 cm with the fish in each interval being regarded as having the midpoint size. The last interval for brown trout includes fish over 47.5 cm in length, while the last interval for rainbow trout includes those over 37.5 cm. These were plotted as though they were in an interval of length 2.5 cm. The total number of brown trout captured by the three anglers was 157, while the electrofishing produced 116 fish in the selected size range (Fig. 1). Only 26 fish were common to both groups. Also, while the anglers captured 17 rainbow trout in sizes 25–41 cm, the electrofishing crew captured 2, with 1 fish common to both groups.

Data on the angler–recapture frequency of fish initially angler captured in the period from 1973 to 1976 inclusive are shown in Fig. 2. These data include only those fish captured and recaptured by the three participating anglers. There was a steadily increasing probability of recapture with increasing length for brown trout and an approximately constant (lower) recapture probability for rainbow trout (Fig. 2).

For both species there is a larger probability that a released fish will be captured during the same season than during the subsequent season (Table 1). For brown trout, roughly 1 out of 5 of the released fish was captured the following season, 1 out of 20 was captured two seasons after, and 1 out of a 100 was captured three or more seasons later. For rainbow trout, 1 out of 10 of the released fish were recaptured the following season and none were recaptured later than that.

The number of times an individual fish may be recaptured after release by an angler is remarkably similar for the two species (Table 2). Roughly one-third of both species released by the three anglers were subsequently recaptured at least once by one of them. After the first capture, the data indicate an exponential decrease in the number of fish versus times captured with an approximate one-half ratio for each capture.

A final point of interest is the movement of angler-captured trout. The angling data indicate that the majority, perhaps as many as 95%, of the larger specimens of brown trout caught by angling in the Mainstream of the Au Sable never move their

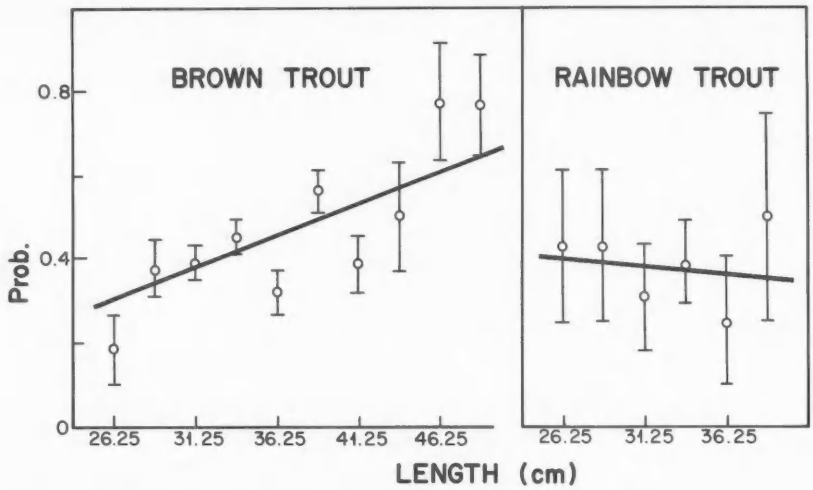

FIG. 2. Probability (relative frequency) of recapture by fly fishermen as a function of length.

TABLE 1. Percentage of angler-captured fish recaptured during the same or later years as a function of the number of seasons between captures.

Length (cm)	% recaptured same year	% recaptured next year	% recaptured 2 yr later	% recaptured 3 or more yr later
		Brown trout		
<35	23.7	19.3	5.5	1.7
≥35	37.4	17.3	3.1	0.8
All	28.5	18.7	4.7	1.4
		Rainbow trout		
<35	32.7	8.6	0	0
≥35	7.7	16.7	0	0
All	27.7	10.6	0	0

TABLE 2. Number of angler-captured fish caught *k* or more times

Brown Trout		Rainbow Trout	
k	No. caught *k* or more Times	*k*	No. caught *k* or more Times
1	378	1	51
2	132	2	16
3	62	3	7
4	28	4	3
5	14	5+	0
6	8		
7	5		
8	3		
9	2		
10	1		
11+	0		

summer feeding stations more than a metre or two from a given location, even over a period as long as 4 yr. On the other hand, distances between locations of successive captures of rainbow trout are typically of the order of tens or even hundreds of metres.

Discussion

There are several explanations for the results represented by Fig. 1 and the fact that only 26 specimens of *S. trutta* were common to the angler-captured and electrofishing-captured groups. We suggest that the anglers and electrofishers captured different subpopulations of this species. Another explanation is that the capture probabilities of both methods were so low that each group captured only a small fraction of the total population. This appears to be ruled out by recapture data which would indicate probabilities for both techniques of 0.3–0.5. The electrofishing probability was estimated by using data taken by the same DNR crew in one of the 100-m sections on two successive days in the fall. Alternatively, these results could stem from the rapid migration of the fish population. This possibility appears to be ruled out by several factors: (i) the electrofishing data were taken in April, a time when brown trout are not expected to be migrating; (ii) the angling data indicate that during the summer months the majority of the larger brown trout caught by angling in the Main Stream of the Au Sable do not move more than a few metres from a given location; (iii) recent angling data (taken after the legalization of winter angling) indicate no large-scale, late-winter movement of brown trout. A somewhat more likely explanation of the inability of each group to recapture the fish caught by the other lies in the nature of the stream itself, and perhaps in the method used for electrofishing. The principle cover for larger specimens of *S. trutta* in the river is either streamside brush or the bottoms of deep holes. The DNR crews were wading and unable to reach fish in the bottom of the two deepest holes and are likely to have been unable to capture fish under the larger collections of brush. It is conceivable that the fish that were out in the open during the day when the DNR crews were fishing were different from those which were out and feeding in the morning, evening, and after dark when the anglers were fishing. In this context, it should be pointed out that the test section of the river has large numbers of rental canoes passing through it every day during the summer months. On weekends the numbers often reach or exceed 100/h during peak periods.

The data on rainbow trout at first seem to be consistent with the removal of that species from the test section of the river by an April spawning run. However, that section of the river is routinely used for spawning by rainbows so that many specimens should have been present during the electrofishing even if they were not the same ones caught by the anglers. Data from winter angling indicate the presence of rainbow trout in that section of the river throughout April. One cannot invoke the presence of brush to hide them from electrofishing because, unlike brown trout, rainbow trout were consistently found in midstream by the anglers. This was true even when canoe traffic was at its peak. The fish simply moved away from their stations as a canoe approached, circled, and returned as it passed. It is probably this behavior which explains the relative inefficiency of electrofishing for capturing this species. The DNR crews often reported seeing them execute the same circling maneuvers as the crew approached with the shocker.

The shapes of the size distributions in Fig. 1 are also of interest. The drop-off at the lower end of each should be ignored, since both the DNR and the three anglers were using a nominal 30-cm minimum length for tagging fish but both tagged some fish below that size. From 30 cm up, each group made every effort to tag every fish captured. Nonetheless, the graphs clearly indicate that the anglers captured a much higher percentage of large fish than did the electrofishers. Probably a large part of this size discrepancy is due to in-season growth of the fish after the electrofishing data were taken. However, brown trout in the Au Sable grow rather slowly (Favro et al. 1979) so that growth cannot be used to explain the entire effect. One should recognize that if the premise that there are coexisting populations in the river is correct, it is also possible that the two populations may have quite different size distributions. In this case the shift of the angler-captured curve relative to the electrofishing curve would not necessarily indicate any preferential capture of larger fish. This suggestion does not seem to be likely in view of the recapture data presented in Fig. 2 which clearly show the preferential recapture of larger fish.

The data given in Tables 1 and 2 appear to be somewhat paradoxical. If three anglers were able to recapture fish 1 or 2 yr, or even 3 yr, after releasing them with a rather high probability, why were these same fish not captured by other anglers and removed from the river before those recaptures? The answer probably lies in the nature of the information obtained by the three anglers in the process of tagging and releasing fish. At the beginning of the experiment the anglers did not know that the larger specimens of brown trout were always to be found in exactly the same location in which they were originally captured. When this became apparent after the tagging and recapture of many fish, the natural reaction was to fish with greater persistence in locations in which large fish were known to be present. Part of the increase in the probability of recapture of brown trout with increasing size by the anglers is undoubtedly due to this tendency.

These considerations do not apply to rainbow trout in the Au Sable. Rainbows have a strong preference for the faster currents of open water and hence do not associate with a particular piece of cover. The distances between the locations of successive captures of *S. gairdneri* are typically of the order of tens or sometimes even hundreds of metres. The lower recapture frequency of this species, as well as the failure of the three anglers to recapture any of them more than 1 yr after the initial capture, may well be due to migration, or removal by other anglers.

Although the discussion given above emphasizes the fact that released trout can be recaptured after quite long intervals of time, it is also of some interest to ask how short an interval might elapse between captures. There were quite a few occasions when a fish was recaptured within a day of the first capture. In one unusual case, a 40-cm-long brown trout was tagged one day and recaptured *twice* the next day, with the latter captures less than 1 h apart! After that the fish was not captured for almost 14 mo.

The most important implication of the data presented here is that the trout captured by electrofishing and the trout caught by angling appear to belong to disjoint subpopulations. This conclusion is certainly not universal. It may be unique to the Au Sable Mainstream. However, it does say that the indiscriminate application of electrofishing data to the solution of angling problems should be regarded as suspect until this two-population possibility has been ruled out.

Acknowledgements

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PERSPECTIVES

Large-Scale Risk Assessment of Acid Rain Impacts on Fisheries: Models and Lessons

C. K. Minns

Great Lakes Fisheries Research Branch, Department of Fisheries and Oceans, Canada Centre for Inland Waters, 867 Lakeshore Road, P.O. Box 5050, Burlington, Ont. L7R 4A6

J. R. M. Kelso

Great Lakes Fisheries Research Branch, Department of Fisheries and Oceans, 1219 Queen Street East, Sault Ste. Marie, Ont. P6A 5M7

and M. G. Johnson

Great Lakes Fisheries Research Branch, Department of Fisheries and Oceans, 1180 20th Street East, P.O. Box 969, Owen Sound, Ont. N4K 6H6

Minns, C. K., J. R. M. Kelso, and M. G. Johnson. 1986. Large-scale risk assessment of acid rain impacts on fisheries: models and lessons. Can. J. Fish. Aquat. Sci. 43: 900–921.

Lakes, streams, and their watersheds in large parts of the world have little ability to neutralize acidity associated with precipitation. Resource management agencies are concerned with the extent of these impacts including the loss/hazard to key fish species, and the likely status of these aquatic systems given alternate emission control scenarios. Two models designed to provide such a large-scale risk assessment are presented herein. The strengths and weaknesses are identified. Since models draw together the best of our theories, experimental, and survey data, these are compared with existing knowledge, theories, and data.

Un peu partout dans le monde, les lacs, les cours d'eau et leurs bassins hydrographiques ont une faible capacité de neutralisation en ce qui concerne l'acidité des précipitations. Les organismes de gestion des ressources s'intéressent à l'ampleur des effets qui découlent de cette situation, notamment aux pertes ou aux dangers touchant les espèces de poissons importantes et à l'état dans lequel se trouveraient vraisemblablement les systèmes aquatiques si on imaginait d'autres scénarios de limitation des émissions. On présente ici deux modèles conçus pour fournir une telle évaluation des risques sur une grande échelle. On identifie les points forts et les points faibles de ces modèles. Comme ces modèles font appel à tout ce qu'il y a de mieux parmi nos théories, nos données expérimentales et nos données d'observation, on les compare aux connaissances, aux théories et aux données existantes.

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The long-range transport of atmospheric pollutants (LRTAP), particularly SO_2 and NO_x, is recognized as one of the major environmental problems confronting the nations of the Northern Hemisphere. Large areas of North America and Europe are at risk because the terrain is acid sensitive and downwind of the emission sources, e.g. smelters, power plants, and car-congested cities. Consideration of the problem has grown largely as a result of concern for fishery resources in lakes and rivers, e.g. the loss of many brown trout (*Salmo trutta*) lakes in Norway and Sweden (Jensen and Snekvik 1972; Dickson 1975) and salmon (*Salmo salar*) rivers on the east coast of Canada (Watt et al. 1983). However, as studies of the problem grew, other concerns for well being of forests, crops, buildings, and human health have arisen.

The lakes, streams, and their watersheds in large parts of eastern North America and Scandinavia have little ability to neutralize the acidity associated with the precipitation containing excess sulphate and nitrate. In response, the alkalinity and pH levels of freshwater may be reduced, thereby threatening fisheries. Fisheries may be affected in a number of ways: (i) enhanced bioaccumulation of some metals, e.g. Hg and Pb (Scheider et al. 1979; Suns et al. 1980; Kelso et al. 1982) that may render fish flesh unsafe for human consumption, (ii) declines in fish production (Farmer et al. 1980; Johnson 1981; Kelso and Gunn 1984), (iii) alteration of community structure (Harvey et al. 1981), (iv) imposition of mortalities from episotic changes in chemistry (Harvey and Lee 1982), (v) extinction of populations and communities (Beamish and Harvey 1972; Mills 1984; Schindler et al. 1985).

In response to the recognized impacts, above, upon fisheries, the Great Lakes Fisheries Research Branch (GLFRB) sought to develop a methodology which would (1) provide an assessment of aquatic chemistry and all fishery resources (presence/absence of key fish species and lake productivity)

FIG. 1. HSM-H study area and location of the 13 quarternary watersheds in Ontario.

on a regional scale and (2) allow predictions of future status given alternate LRTAP management scenarios. We realized that several iterations would be necessary before a fully acceptable methodology would be achieved. Minns (1981) used the lake inventory database of the Ontario Ministry of Natural Resources (OMNR) to predict the risk for all lakes in Ontario. His approach was based on the nomogram analysis of Henriksen (1979). In 1980, a contract was awarded to Hough, Stansbury and Michalski Ltd. and J. E. Hanna Assoc. Inc. (HSM-H) to design, assess, and apply a methodology which would (i) determine qualitatively and quantitatively those game fish assemblages in acid-vulnerable inland Ontario lakes, (ii) estimate their current productivity, and (iii) predict their potential rate of change under various acid deposition rates. In 1982, GLFRB sponsored an Adaptive Management Modelling Workshop (Holling 1978) facilitated by Environmental and Social Systems Analysts Ltd. (ESSA) with the objectives of (1) developing a preliminary model of regional scale impacts from acid deposition and (2) identifying information needs to improve such a model.

The models from these two efforts are analyzed and compared herein. Their strengths and weaknesses are identified. Finally, these models are assessed against other efforts to predict impacts.

HSM-H Model

HSM-H confined the analysis to those areas of Ontario with low levels of soluble carbonates in the soil and/or bedrock, the Canadian Shield (Fig. 1). They developed physico-chemical and fisheries models, the linkage between these models, and the framework for extrapolation (Fig. 2).

Physico-Chemical Model

The approach is based on an annual alkalinity or acid neutralizing capacity (ANC) budget for a lake/watershed system. ANC sources include overland runoff, groundwater, net autochthonous (internal) alkalinity production, and residual lake alkalinity. Hydrogen ion inputs to a lake are balanced against the pool of ANC on an annual basis and a final lake ANC calculated. The outcome is converted to lake alkalinity concentration via a hydrologic budget. The pH of lake water is derived via a predictive equation, and the model assumes a complete mixing, single input − single discharge, fixed volume reactor:

$$(1)\quad [A_L]t+1 = \frac{[A_L]_t V_L + [A_R]_t V_R + [A_A]V_{EZ} - [H^+]V_{PL}}{V_L + V_R + V_G + V_{PL} - V_{EL}}.$$

At steady state:

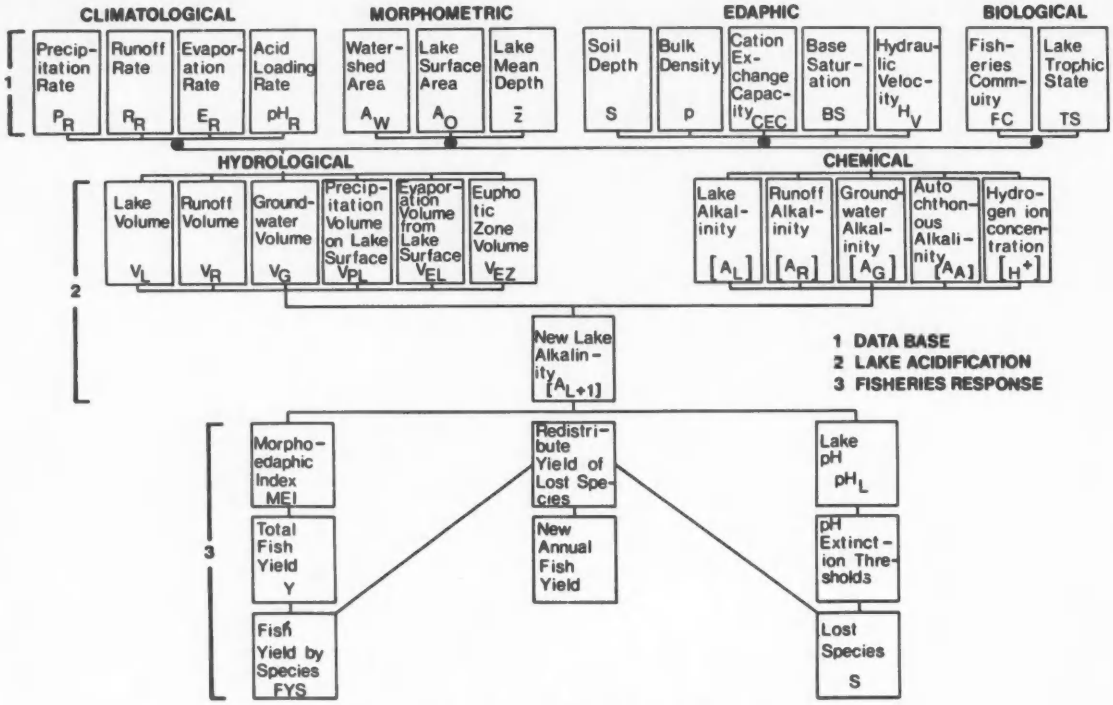

FIG. 2. Analytical framework for the HSM-H model.

$$(2)\quad [A_L] = \frac{[A_R]V_R + [A_G]V_G + [A_A]V_{EZ} - [H^+]V_{PL}}{V_R + V_G + V_{PL} - V_{EL}}.$$

In model simulations, it was assumed that every lake was in equilibrium with initial conditions. The derivation of all components in Equations (1) and (2) is given in Table 1.

Fisheries Model

A general method of predicting potential total fish yield per year is the morpho-edaphic index (MEI) developed by Ryder (1965) and Ryder et al. (1974):

$$(3)\quad \text{MEI} = \text{TDS}/\bar{z}$$

where TDS is total dissolved solids (milligrams per litre), $\bar{z}$ is mean depth of the lake (metres), and yield = $1.378(\text{MEI})^{0.4461}$. Ryder's (1965) original data base showed that TDS was 1.54 times alkalinity (milligrams per litre) on average. Therefore, it was assumed that an alternative yield prediction could be developed using alkalinity. Thus, when alkalinity declined, potential yield would decline also.

Once an estimate of total yield is obtained, a portion is allocated (Table 2) to the game fish assemblage in a lake (Adams and Olver 1977; R. A. Ryder, OMNR, Thunder Bay, Ont., pers. comm.).

In addition to the linkage of overall yield and alkalinity, the apparent pH extinction thresholds of various species were incorporated: 5.7 for bass (*Micropterus* species), 5.5 for lake trout (*Salvelinus namaycush*), brook trout (*S. fontinalis*), and walleye (*Stizostedion vitreum vitreum*), and 4.7 for northern pike (*Esox lucius*) (Beamish 1974, 1975, 1976; Beamish et al. 1976; Menendez 1976; Keller 1978; Beamish and Harvey 1972; Vallin 1953). When species becomes extinct, a portion of its yield is reallocated to the remaining species (Table 2). Nine different fish assemblages were considered (Minns 1981).

Scaling and Implementation

Given the delineated study area (Fig. 1), 30 quaternary watersheds (terminology used by Water Survey of Canada) were selected from the secondary watersheds making up the total area. In some secondary watersheds, more than one quaternary watershed was used if it was heterogeneous with respect to soil cover, bedrock, lake characteristics, and other factors.

When available counts and measures (Cox 1978) were compared with topographic sheets, some errors were found. Also, measures of watershed area were not available. Therefore, for each of the 30 quaternary watersheds, the lake area and watershed area were determined using a digital planimeter for every lake present. In all, 6988 lakes and their watersheds were measured; of these, 3059 were considered by local OMNR staff to have game fish species present.

For lakes that had been inventoried by the OMNR, data on mean depth and the game fish assemblage were used. Further, staff at OMNR district offices were consulted for advice, particularly to identify the fish assemblages.

In order that results from the small watersheds could be extrapolated to the larger units, scalars (SC) were calculated. The scalars are the ratio of the area of the secondary watershed to the area of the watershed unit which had been measured. For lakes with brook trout present, a different scalar was used (Minns 1981) to compensate for the inventory bias toward that species.

The individual lakes within a watershed were then assigned

TABLE 1. Components of the physico-chemical and biological submodels.

Component	Description	Units	Theory/assumptions	Sources of data
V_L	Lake volume $A_0 \cdot \bar{z} \cdot 10^7$	L	Calculation	
A_0	Lake area	ha		
$\bar{z}$	Lake mean depth	m		
$[A_R]$	Runoff alkalinity exp $(pH_R - pK - pCO_2)$	$eq \cdot L^{-1}$	Is a function of soil cation exchange capacity and base saturation, and in equilibrium with atmospheric CO_2	Kramer et al. 1979
pK	Bicarbonate system rate constant		Constant = 7.82	
pCO_2	Log_e partial pressure CO_2		Constant = 3.00	
pH_R	pH of runoff $pH_R = 3.03BS_t + 4.55$		pH of runoff is a linear function of soil base saturation (BS) in years t	Kramer et al. 1979
BS_t	Soil base saturation $\frac{kBS - [H^+]V_{PW}}{k}$ where $k = A_W \cdot S \cdot \rho \cdot CEC \cdot 10^8$	None	Base saturation is a function of amount of soil and cation exchange capacity and can be depleted by acid load to the watershed	
A_W	Watershed area	ha		
S	Soil depth, active layers	cm	A constant used for all areas	
ρ	Bulk density of soil	$g \cdot cm^{-3}$	A constant either 1.4 or 1.5 depending on area	
CEC	Cation exchange capacity	$eq \cdot g^{-1}$	A constant in each area ranging from 0.00010 to 0.00020	Bolt and Bruggewert 1978: kaolinite 2–80 $\mu eq \cdot g^{-1}$; illite 150; montmorillonite 800; humus 2000–3000
V_{PW}	Annual rainfall volume falling on watershed $A_W \cdot P_R \cdot 10^5 = R_R \cdot A_W \cdot 10^5$	$L \cdot yr^{-1}$	Calculation	
V_R	Annual runoff volume	$L \cdot yr^{-1}$	Calculation	
R_R	Unit runoff	$cm \cdot yr^{-1}$	Each watershed has a fixed unit runoff	Pentland 1968
$[A_G]$	Groundwater alkalinity	$eq \cdot L^{-1}$	Groundwater generally has high pCO_2 and high contact overburden; a constant value used 2×10^{-3} $eq \cdot L^{-1}$, a value typical for shallow to moderate depth groundrates aquifers	Wang and Chin 1978
V_G	Groundwater inflow $\bar{z} \cdot \sqrt{A_0} \cdot H_V (10^{-0.6 - \frac{A_0}{A_W}}) \times (P_R/80) \times 3.1536 \cdot 10^{10}$	$L \cdot yr^{-1}$	Modification of Darcy's equation; water is assumed to enter the lake across on interface $(\bar{z} \cdot \sqrt{A_0})$ with a velocity H_V, a scaling factor $(10^{-0.6 - \frac{A_0}{A_W}})$, a precipitation scalor relative to mean of 80 $cm \cdot yr^{-1}$, and a units scalar	
H_V	Hydraulic velocity of soils in watershed	$cm \cdot s^{-1}$	One of two values was used depending on the area (0.0001 or 0.00001)	
P_R	Precipitation rate	$cm \cdot yr^{-1}$	Fixed rate for each watershed	AES meteorological records
$[H^+]$	Hydrogen ion content of precipitation	$eq \cdot L^{-1}$	Calculated from recorded annual mean pH values; Acid effects of particulates were ignored	Cowling 1981; Wisniewski and Keitz 1983
V_{PL}	Annual rainfall volume on lake $P_R \cdot A_0 \cdot 10^5$	$L \cdot yr^{-1}$	Calculation	
$[A_A]$	Autochthonous alkalinity contribution	$eq \cdot L^{-1} \cdot yr^{-1}$	If primary production uses NO_3 as the primary N source, H^+ is also consumed. Evidence for this occurring in the summer has been presented by Zimmerman and Harvey (1979) and Dillon et al (1980). An equivalence between gross	Fee 1980; Johnson et al. 1970; Michalski and Conroy 1973; (annual primary production in Ontario Shield lakes)

TABLE 1. (*Concluded*)

Component	Description	Units	Theory/assumptions	Sources of data
			primary production at alkalinity generation was obtained via the Redfield–Ketchum–Richards phytoplankton equation and net production is set at 59% of gross. Values used range from 17 to 236 $eq \cdot L^{-1} \cdot yr^{-1}$. P. J. Dillon (pers. comm) suggests unproductive lakes may have values from 10 to 15	
V_{EZ}	Volume of euphotic zone $EZ \cdot A_0 \cdot 10^7$	L	This is the volume in which the net autochthonous alkalinity generations is presumed to occur	
EZ	Depth of euphotic zone	m	Fixed values ascribed to each of nine fish assemblage types	
V_{EL}	Volume of evaporation from lake $E_R \cdot A_0 \cdot 10^5$	$L \cdot yr^{-1}$	Calculation	
E_R	Unit evaporation rate	$cm \cdot yr^{-1}$	Fixed unit rates assumed for each area	Pentland 1968
A_W/A_0	Drainage to lake area ratio	—	Calculation	

TABLE 2. Model parameter values for Ontario fish assemblages. (NP, northern pike; BA, bass; WA, walleye; LT, lake trout; BT, brook trout; (1), annual primary production ($g\ C \cdot m^{-3} \cdot yr^{-1}$); (2), alkalinity generation ($\mu eq \cdot L^{-1} \cdot yr^{-1}$); (3), euphotic zone (m); (4), proportion of total MEI yield; (5), % of lost species yield taken up by remaining species).

	Autochthonous alkalinity			Fish yield allocation: initial (4)					Yield take up at pH thresholds (5)	
Fish assemblage	(1)	(2)	(3)	NP	BA	LT	BT	WA	pH 5.7	pH 5.5
1. NP – BA – WA	15	126	3	0.10	0.06	—	—	0.24	70	50
2. NP	12	100	4	0.40	—	—	—	—	—	—
3. NP – WA	12	100	4	0.20	—	—	—	0.20	50	—
4. LT – NP – BA – WA	10	84	8	0.05	0.03	0.20	—	0.12	80	30
5. LT	2	17	16	—	—	0.25	—	—	—	—
6. LT – NP – WA	8	67	8	0.06	—	0.15	—	0.09	40	—
7. BT	5	42	10	—	—	—	0.30	—	—	—
8. BT – LT – BA	5	42	10	—	0.04	—	0.15	0.09	70	—
9. No game fish	—	—	—	—	—	—	—	—	—	—

TABLE 3. Lake–watershed parameter categories assigned for the purposes of a model run.

Category	Lake area (A_0) (ha)	Watershed area (A_W) (ha)	Mean depth ($\bar{z}$) (m)
1	—	—	2.5
2	50 000	50 000	7.5
3	5 000	5 000	14.5
4	500	500	
5	50	50	
6	5	5	
7	0.5	0.5	

a fish assemblage (Table 2) and morphometric (Table 3) parameters. In model simulations, the main nonlake parameters were specified for each watershed (Table 4). Initial lake alkalinity was assumed to be a steady state with respect to the initial precipitation pH. The average pH of precipitation was used to calculate acid loading rather than sulphate. Given a scenario, i.e. a trend in precipitation pH over time, each lake's alkalinity budget was recalculated on an annual time step. Results were stored for time 0, 5, 10, 20, and 40 yr, representing the period from 1980 to 2020. The results were aggregated by fish community and lake area categories. The results for the sampled watersheds were then multiplied by the scalars to give results for secondary watersheds. Thus, the sample of lakes in a quaternary watershed was taken to be representative of a larger region.

Results

The model was run under three different scenarios: constant precipitation pH, increasing precipitation pH (+0.4 units over 20 yr and then level), and decreasing precipitation pH (−0.4 units over 20 yr and then level). Model results were in tabular form, but can be expressed as isopleths of fish yield change (relative to time zero) on maps, e.g. after 40 yr with a lower precipitation pH scenario (Fig. 3). Such results were taken to be an indication of what could be expected rather than adequate predictions of impact.

We also attempted to calibrate the model by way of predicting current alkalinity in a set of lakes. This was not success-

FIG. 3. Losses in game fish yields with a low pH scenario over a 40-yr period.

ful, since the data needed to parameterize the model for any single lake were not available.

ESSA Model

In the acidic precipitation context, there were two adaptive management workshops which predated ours. One was conducted by the U.S. Fish and Wildlife Service (Andrews et al. 1980), which focused on the detailed chemical and biological simulation of a single watershed–lake complex. The other was convened by OMNR (Marmorek et al. 1982), which examined the link between acidic precipitation and fisheries management in a small number of lakes in the Algonquin region of Ontario. Neither of these workshops considered the problems of extrapolation to regional scale impacts.

This model predicts changes in the fisheries' yield for key eastern Canadian species, based on a knowledge of acid deposition rates and aspects of a lake or river's physiography, e.g. watershed size, annual precipitation, etc.

The model structure includes two levels (Fig. 4). The first level, the "Site" model, made predictions about changes in the chemistry and fish of an individual lake or river. For regional predictions, the site models were embedded within a second level, called the "Scaling" model, which used the site models to make predictions for a range of lake (or river) types and then aggregated them to the regional level. The predictions were made on a yearly basis for 30–50 yr.

Chemical Site Model

The chemistry submodel computed changes over time in precipitation and acid deposition and, in the lake or river, alkalinity, pH, and aluminum concentration. For each year of the model run, the chemistry submodel performed a series of operations, summarized in Fig. 5 and outlined in Table 5.

Fish Site Model

Loss in fish yield was used as the key indicator of acidification impacts; thus, the model was designed to predict yield and its response to changes in lake chemistry. The fish submodel thus received mean and spring pH and labile, monomeric aluminum concentrations from the chemistry submodel in order to compute changes over time in fish yield. Since lake chemistry changes did not affect yield directly, but rather, influenced yield through population processes such as recruitment and survival rates, the model allowed the user to explore these impli-

TABLE 4. Input data for the lake acidification model by watershed unit.

Watershed unit	pH scenarios			Base saturation (%)	Cation exchange capacity ($eq \cdot g^{-1}$)	Runoff (cm)	Precipitation (cm)	Evaporation (cm)	Hydraulic velocity ($cm \cdot s^{-1}$)	Bulk density ($g \cdot cm^{-3}$)
	High	Medium	Low							
2AA-3	4.4	4.8	5.2	0.4	0.00020	31.0	71.1	55.9	0.00001	1.5
2AB-6	4.4	4.8	5.2	0.25	0.00016	31.0	71.1	53.3	0.00010	1.4
2BA-6	4.4	4.8	5.2	0.15	0.00010	37.9	81.3	50.8	0.00010	1.4
2BB-2	4.4	4.8	5.2	0.15	0.00010	37.9	86.4	50.8	0.00010	1.4
2BD-10	4.1	4.5	4.9	0.15	0.00010	44.8	81.3	48.3	0.00010	1.4
2CC-8	4.1	4.5	4.9	0.15	0.00010	30.5	81.3	50.8	0.00010	1.4
2CF-7	4.3	4.7	5.1	0.10	0.00010	37.9	81.3	53.3	0.00010	1.4
2OC-7	4.2	4.6	5.0	0.15	0.00010	44.8	81.3	50.8	0.00010	1.4
2EA-19	4.1	4.5	4.9	0.32	0.00014	51.7	101.6	66.0	0.00010	1.4
2EA-22	4.0	4.4	4.8	0.32	0.00014	51.7	101.6	66.0	0.00010	1.4
2EB-10	4.0	4.4	4.8	0.32	0.00014	48.3	101.6	66.0	0.00010	1.4
2HL-5	3.9	4.3	4.7	0.32	0.00014	34.5	86.4	68.6	0.00010	1.4
2JE-15	4.2	4.6	5.0	0.40	0.00020	44.8	81.3	50.8	0.00001	1.5
2KD-3	4.0	4.4	4.8	0.32	0.00014	34.5	86.4	63.5	0.00010	1.4
4CB-9	5.4	5.8	6.2	0.20	0.00014	29.3	63.5	50.8	0.00010	1.4
4DA-27	5.3	5.7	6.1	0.20	0.00014	32.7	63.5	50.8	0.00010	1.4
4FA-25	4.9	5.3	5.7	0.20	0.00014	31.0	71.1	45.7	0.00010	1.4
4GA-15	4.7	5.1	5.5	0.25	0.00016	29.3	73.7	61.0	0.00001	1.4
4GE-15	5.0	5.4	5.8	0.25	0.00016	32.7	71.1	45.7	0.00001	1.4
4JC-1	4.3	4.7	5.1	0.25	0.00016	37.9	76.2	45.7	0.00010	1.4
4LA-5	4.3	4.7	5.1	0.32	0.00020	37.9	76.2	45.7	0.00001	1.5
4LK-6	5.1	5.5	5.9	0.45	0.00024	37.9	76.2	45.7	0.00001	1.5
4MB-4	4.3	4.7	5.1	0.45	0.00024	41.4	81.3	50.8	0.00001	1.5
5PB-7	4.7	5.1	5.5	0.20	0.00014	20.7	68.6	58.4	0.00010	1.4
5PO-7	5.0	5.4	5.8	0.20	0.00014	20.7	63.5	56.4	0.00010	1.4
5PE-01	5.1	5.5	5.9	0.15	0.00010	20.7	61.0	58.4	0.00010	1.4
5QA-5	4.7	5.1	5.5	0.20	0.00014	27.6	76.2	58.4	0.00010	1.4
5QC-2	5.2	5.6	6.0	0.32	0.00020	27.6	61.0	55.9	0.00001	1.5
5QB-8	5.1	5.5	5.9	0.32	0.00020	29.3	63.5	55.9	0.00001	1.5
5RC-6	5.3	5.7	6.1	0.15	0.00010	27.6	61.0	55.9	0.00010	1.4

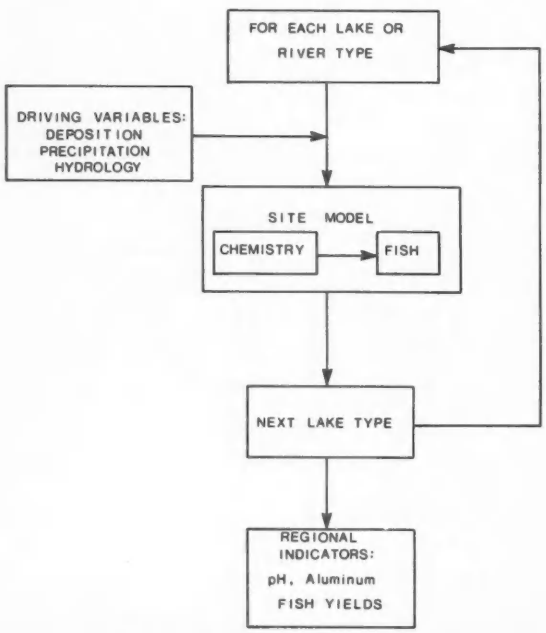

FIG. 4. General structure of the ESSA model.

cations and how they were affected. Details of the operations are outlined in Table 6.

Scaling Model

The final stage of model development was to embed the chemical and fish site models into a structure which would scale prediction for an individual lake type to a regional level. This scaled model would repeatedly run the site model for a large set of different lake or river types deemed representative of the diversity of lakes or rivers in a region. Based on the proportion of the total area of lakes or rivers in the region, the scaling model calculates the total resource loss.

The first step was to specify the information required about a lake or river to define its type: (1) acid deposition rate or rain pH, (2) mean annual precipitation and range, (3) hydrograph peak to mean flow ratio, (4) lake or river area, (5) watershed area, (6) mean depth, (7) reference alkalinity generation and change in generation with change in pH, and (8) lake DOC level. In addition to mean depth, the fish submodel required (9) lake total dissolved solids (TDS) and (10) the present fish assemblage. The first three quantities, above, were assumed to be uniform within a given region.

The next step was to consider the range of values observed in a region for each of the criteria (except the last) and divide that range into a small set of classes. Since three classes were defined for each of criteria 4 through 9, and criterion 10 had 11 classes (i.e. lake assemblages), the total number of lake

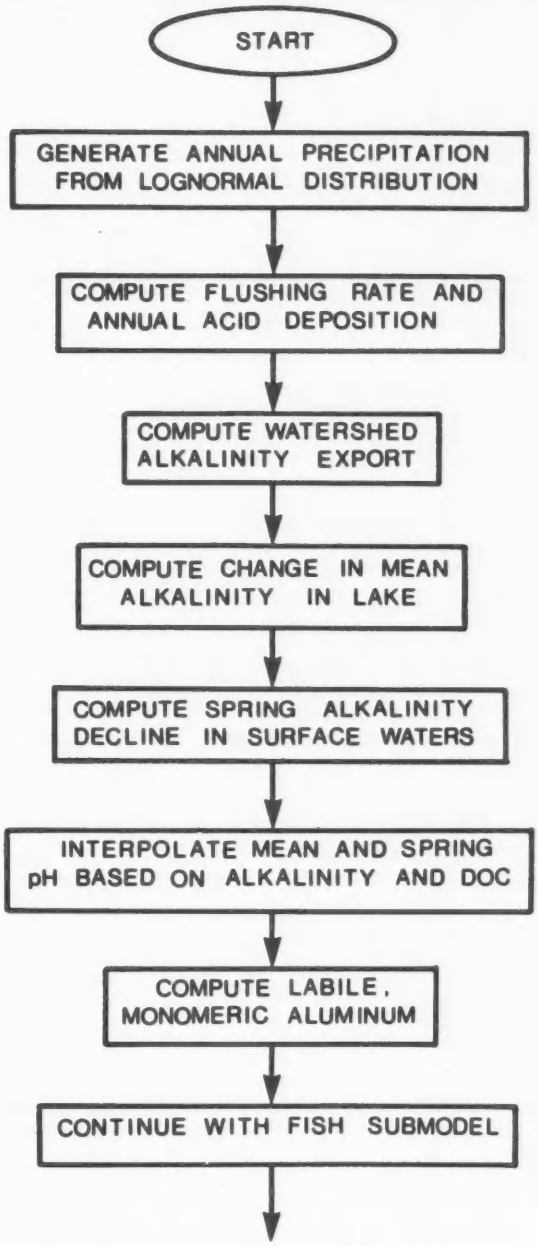
START
GENERATE ANNUAL PRECIPITATION FROM LOGNORMAL DISTRIBUTION
COMPUTE FLUSHING RATE AND ANNUAL ACID DEPOSITION
COMPUTE WATERSHED ALKALINITY EXPORT
COMPUTE CHANGE IN MEAN ALKALINITY IN LAKE
COMPUTE SPRING ALKALINITY DECLINE IN SURFACE WATERS
INTERPOLATE MEAN AND SPRING pH BASED ON ALKALINITY AND DOC
COMPUTE LABILE, MONOMERIC ALUMINUM
CONTINUE WITH FISH SUBMODEL

FIG. 5. Flow of annual operations in the chemical site model.

types was $3 \times 3 \times 3 \times 3 \times 3 \times 3 \times 11 = 8019$. The overall structure of the scaled model is depicted in Fig. 6.

Results

Scaling

Since the scaling process involved the analysis of large amounts of data, much of which were not available, parameters were collected where available and applied to the Muskoka–Haliburton area as a test region.

Data were readily available from the Experimental Lakes Area (ELA) near Kenora, Ontario (Watershed 5PD from Cox 1978). Table 7 reflects the size distribution of lakes, ratio of A_W/A_0, mean depth, dissolved organic carbon (DOC), and TDS. The effect of melding data from the ELA with the Muskoka–Haliburton area is unknown. Input parameters adapted specifically for Muskoka–Haliburton are given in Table 8.

Model output

When the model was run with current deposition rates (67 meq·m^{-2}·yr^{-1}) from CANSAP (a precipitation monitoring system operated by Environment Canada), the three major fish communities (Table 9) maintained yields at initial levels (Fig. 7A, 7B, and 7C). A small decline in yield of the three communities actually occurs early in the simulation as a consequence of two successive years of heavy precipitation (randomly generated, see Table 5). However, the losses are not sustained. Yields were 0.51 for brook trout, 0.27 for lake trout, and 0.57 kg·ha^{-1}·yr^{-1} for whitefish (*Coregonus clupeaformis*).

Increasing deposition rates by 50% to 99 meq·m^{-2}·yr^{-1} causes substantial declines in the yields of all species (Fig. 7A, 7B, and 7C). Lake trout and lake whitefish yields both decline, but at somewhat different rates. The form of the decline curves is a consequence of the lake types inhabited by each species. Brook trout (Fig. 7A) inhabiting smaller lakes (Table 9) demonstrate a quite different response pattern from the other two species (Fig. 7B and 7C). It appears that lakes in which only brook trout are found undergo year-to-year variations in pH which sometimes result in recruitment failures. Inspection of data shows that recruitment failures are occurring in years of heavy precipitation (i.e. deposition).

Trends in pH for two types of lakes are depicted in Fig. 7D and 7E. The first (Fig. 7D), a small, shallow lake with a small watershed, acidifies rapidly under the high deposition scenario. The constant pH levels after year 5 are a consequence of the way the model calculates pH from alkalinity. If alkalinities are less than -100 μeq·L^{-1}, the pH is set to be the minimum value on the titration look-up table. Actual pH values may get lower; however, the impact of reduced pH on the biota has long since been felt when this point is reached. When current deposition rates are imposed, pH fluctuates substantially in response to variations in precipitation (Table 5, random variate). It is probably this type of fluctuation which is responsible for the transient declines in yield of all three species in the baseline scenario.

The second lake type (Fig. 7E) is large, deep, and with a small watershed. This lake acidifies much more slowly than does the previous type.

A useful indicator of the overall state of a region with respect to acidification is the total area of lakes with a pH less than some "critical" value (Fig. 7F). This figure indicates that more than half of the total area of lakes acidify rapidly when deposition is increased (brook trout type lakes), while the remaining lakes only do so in years of heavy precipitation.

Analysis of the Models

Hydrological Component

Both models consider all lakes as headwaters. The models are similar in many respects. Calculation of lake flushing rate is used as a basis for comparison.

TABLE 5. Chemistry submodel.

Component	Description	Units
P_t	Annual precipitation in year t $P_t = \bar{P} \cdot e^{z \cdot s}$	m
$\bar{P}$	Mean annual precipitation	m
Z	Random variate from $N(0, 1)$	
SD	Standard deviation of annual precipitation	m
ρ	Flushing rate $\rho = \frac{Q}{V} = \frac{P \cdot WR \cdot (A_w + A_o)}{\bar{z} \cdot A_o}$	
Q	Annual outflow	$m^3 \cdot yr^{-1}$
V	Lake volume	m^3
P	Annual precipitation	m
WR	Ratio of outflow to precipitation WR = 1.0 − fraction evaporated + evapotranspired	
A_o	Lake area	ha
A_w	Land area of lake basin	ha
$\bar{z}$	Mean depth	m
D	Annual rate of acid deposition $D = -10^{-pH} \cdot P \cdot 1000$ where $D = -1 \times$ annual acid deposition, pH = mean pH of precipitation (m) (user specifies), P = mean annual precipitation (user specifies), 1000 = conversion factor to μeq	$meq \cdot m^{-2} \cdot yr^{-1}$ of alkalinity or acid
	Watershed alkalinity export	
AAG	Actual alkalinity generation $AAG = RAG \cdot (1 + (E - 1) \cdot 10^{3.5 - pH})$	$meq \cdot m^{-2} \cdot yr^{-1}$
RAG	Reference alkalinity generation	$meq \cdot m^{-2} \cdot yr^{-1}$
E	E = alkalinity generation with pH 3.5 rain/ alkalinity generation with pH 5.6 rain (RAG)	

Units	Theory/assumptions	Source
	A random variate (z) is generated from a normal distribution with mean 0 and SD of 1. Equation generates P, figures following a log-normal probability distribution	
	User specifies for the site	
	User specifies ρ is the number of times per year the lake's volume is replaced	
	User specifies	
	User specifies User specifies User specifies	
$^{-2}\cdot yr^{-1}$ alinity d	User may specify either a constant annual rate of acid deposition ($meq\cdot m^{-2}\cdot yr^{-1}$ of acid) or a rain pH. The rain pH is used in the equation where deposition is expressed in units of negative alkalinity. It is preferable to specify a rain pH so variations in P are considered. P. J. Dillon (pers. comm.) suggests that the mean pH in wet years is as low or lower than the pH in dry years	
	The net export of alkalinity from a watershed equals the alkalinity generated (AAG) minus the annual acid deposition	
$^{-2}\cdot yr^{-1}$	AAG is the potential of a lake or river watershed to neutralize atmospheric deposition (more usually called acid neutralizing capacity (ANC))	
$^{-2}\cdot yr^{-1}$	User hypothesizes what quantity of alkalinity is available to neutralize acidic inputs when the mean pH of precipitation is 5.6 (clean rain)	
	User hypothesizes how the watershed's alkalinity generation will change as the pH of precipitation decreases (E). A pH of 3.5 was assumed to be close to the minimum annual mean pH of P likely to be ever observed	

TABLE 5. (*Continued*)

Component	Description	Units
Alk_{ss}	Steady-state alkalinity $$Alk_{ss} = \frac{D + \left(\frac{r}{r+1}\right) AAG}{P \cdot WR}$$	
r	Watershed to lake ratio $$r = \frac{A_W}{A_0}$$	
$AAG_{current}$	Current alkalinity generation $$AAG_{current} = [Alk_{ss} \cdot P \cdot WR - D]\left(1 + \frac{1}{r}\right)$$	
$\Delta\overline{Alk}$	Annual change in mean alkalinity $$\Delta\overline{Alk} = \frac{D + (A_W/A_0) \cdot (AAG + D)}{\bar{z}} - \rho \cdot \overline{Alk}_t + \overline{Alk}_{int}$$	
$\overline{Alk}_t$	Previous year's mean alkalinity	
$\overline{Alk}_{int}$	Net internal generation of alkalinity per year	
$\Delta\overline{Alk}_{month}$	Episodic alkalinity decline $$\Delta\overline{Alk}_{month} = \frac{FD + (A_W/A_0) \cdot (FG + FD)}{ZS} - \frac{(FQ)}{V} \cdot \overline{Alk}_t + \overline{Alk}_{int}$$	
FD	The fraction of annual deposition occurring during the month.	
$[OH^-]$	$[OH^-] = \frac{K_W}{[H^+]}$	
K_W	Dissociation constant	

its	Theory/assumptions	Source
	Assuming that deposition and alkalinity generation remain constant	
	The fraction $r/(r + 1)$ will increase asymptotically, approaching 1 as r increases; therefore, higher watershed to lake area ratios should yield higher steady-state alkalinities	
	This equation can be used to back-calculate current alkalinity generation assuming the lake/river alkalinity is in equilibrium with its basin. D is negative; therefore, the term in square brackets is always ≥ 0. The level of AAG calculated is the amount required to just maintain current alkalinity levels	
	Larger watershed to lake area ratios will increase $\Delta\overline{\text{Alk}}$ if (AAG + D) is positive but decrease $\Delta\overline{\text{Alk}}$ if (AAG + D) is negative	
	If $\rho = 1$, the annual $\Delta\overline{\text{Alk}}$ will be the sum of within-year changes	
	Model uses a within-year time step short enough to keep $\rho < 0.2$ for each time step	
	Zero net internal generation of alkalinity is assumed	
	If year's mean alkalinity is negative, then the flushing term will make a positive contribution to $\Delta\overline{\text{Alk}}$	
	Alkalinity declines are commonly observed during spring in Ontario and during fall storms in the Maritimes. The $\Delta\overline{\text{Alk}}$ equation is converted to a monthly time step. The episodic alkalinity minimum calculated is not the absolute minimum, but is the mean alkalinity in the mixing zone during the month of minimum alkalinity	
	Constant = 0.57	Jeffries et al. 1979 (figure is average from 3 Ont. lakes)
	Constant = 10^{-14}	Stumm and Morgan 1970

TABLE 5. (*Concluded*)

Component	Description	Units
$[RCOO^-]$	Concentration of organic base $[RCOO^-] = \frac{K_A[C_t]}{[H^+] + K_A}$	
K_A	Dissociation constant	
$[C_t]$	Dissolved organic carbon (DOC) in acid/base equivalents $[C_t] = (2.62 \cdot 10^{-6}) \cdot DOC\,(mg \cdot L^{-1}) + (7.63 \cdot 10^{-6})$	
Al_{free}	Labile, monomeric aluminum (free) $Al_{free} = Al_{total} - Al_{organic} - Al_{colloidal}$	$mg \cdot L^{-1}$
Al_{total}	$Al_{total} = 10^{(5.54 - 0.68\ pH)}$	
$Al_{organic}$	$Al_{organic} = -88 + (54.9 \cdot DOC)$	
$Al_{colloidal}$	Colloidal aluminum	
FG	The fraction of annual alkalinity generation (AAG) in the month	
FQ	The fraction of annual outflow (Q) in the month (affects ρ)	
ZS	The mean mixing depth during the month	
Mean and spring pH	Calculation of pH from alkalinity and DOC $Alk = [HCO_3^-] + 2 \cdot [CO_3^{2-}] + [OH^-] + [RCOO^-] - [H^+]$	
Alk	Total alkalinity	$eq \cdot L^{-1}$
$[HCO_3^-]$	$[HCO_3^-] = \frac{K_H K_1 pCO_2}{[H^+]}$	
K_H	Dissociation constant	
K_1	Dissociation constant	
pCO_2	Solubility of CO_2 in water	
$[CO_3^+]$	$\frac{[CO_3^+] = K_2[HCO_3^-]}{[H^+]}$	
K_2	Dissociation constant	

Units	Theory/assumptions	Source
		C. T. Driscoll, cited in Andrews et al. 1980
	Constant = $10^{-4.41}$ User specifies DOC concentrations	C. T. Driscoll, cited in Andrews et al. 1980
-1	Calculation. Al_{free} is never less than zero	
	Total aluminum was assumed to depend only on pH and was estimated from a regression equation fitted to data from the Adirondack lakes	U.S.–Canada Memorandum of Intent, 1981
	Organic aluminum was estimated from DOC, according to regression equation. Assumes that $Al_{organic}$ is always less than or equal to $Al_{total} - Al_{colloidal}$	C. T. Driscoll, cited in Andrews et al. 1980
	Constant = 20 ppb. Based on concentrations C. Driscoll (pers. comm.) found in Adirondack lakes of between 20 and 50 ppb	
	Constant = 0.25. Is less than FD to reflect short contact time with basin soils during spring melt or fall storm events	Best guess
	Constant = 0.45	Same as above
	Constant = 1.5. Is less than the mean depth due to winter inverse stratification. Lakes or rivers with fall episodic declines would likely have greater mixing depths	Best guess
	Mean and episodic pH values are interpolated from their respective alkalinities, dissolved organic carbon (DOC) concentrations, and assumed saturation of atmospheric CO_2	
1	User specifies	
	Constant = $10^{-1.5}$	Stumm and Morgan 1970
	Constant = $10^{-6.3}$	Stumm and Morgan 1970
	Choice of using titration curves consistent with aqueous CO_2 concentrations of 1.0, 2.25, or 10 times	Beamish et al. 1976; Thompson 1982
	Atmospheric CO_2 (pCO_2 = 3.5, 3.1, or 2.5, respectively). Model run assumed aqueous CO_2 equals atmospheric CO_2	
	Constant = $10^{-10.3}$	Stumm and Morgan 1970

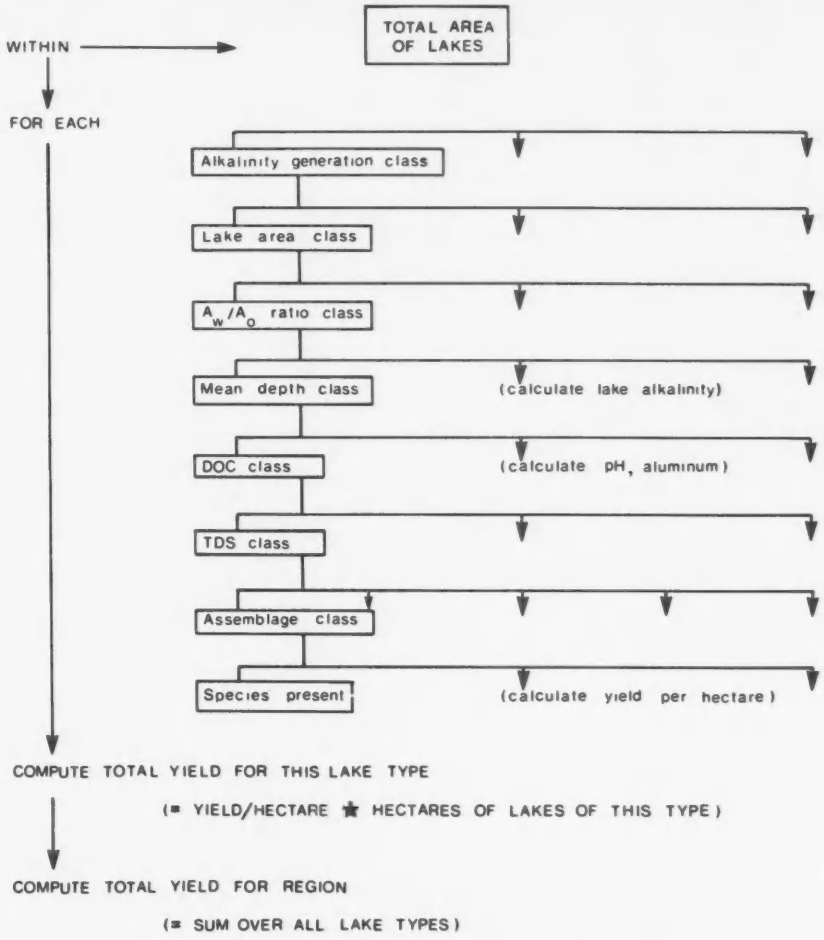

FIG. 6. Schematic representation of the scaled model structure.

The HSM-H model is more elaborate than the ESSA one. It distinguishes between stream and groundwater flows and explicitly considers evaporation from the lake surface. The flushing rate is as follows:

$$\text{Flushing rate} = \frac{\text{Runoff} + \text{groundwater} + \text{precipitation to lake} - \text{lake evaporation}}{\text{Lake volume}}$$

$$= \frac{R_R A_W \cdot 10^5 + V_G + P_R A_0 \cdot 10^5 - E_R A_0 \cdot 10^5}{\bar{z}\, A_0 \cdot 10^7}.$$

For the thirty watersheds selected, precipitation, runoff, and evaporation values were selected from Pentland (1968). The frequency distributions of the ratios R_R/P_R are bimodal (Table 10). Further, in every watershed, $R_R + E_R > P_R$, which implies that terrestrial evapotranspiration ($P_R - R_R$) is less than lake evaporation. Newbury and Beaty (1980) argue that on the Shield in northwest Ontario, $R_R + E_R = P_R$. Groundwater makes an insignificant contribution to the budget. So through the use of ratios $R_R/P_R = k_R$ and $E_R/P_R = k_e$ (expected to equal $1 - k_R$), the equation given above can be greatly simplified to

$$\text{Flushing rate} = \frac{P_R}{\bar{z}}\left(k_R \frac{A_W}{A_0} + 1 - k_e\right)$$

$$= \frac{P_R k_R}{\bar{z}}\,(A_W + A_0)/A_0.$$

Clearly in HSM-H, annual precipitation is the most important variable. It was not varied in the model scenarios even though it is known that there is significant year-to-year variation.

In the ESSA model, precipitation is varied randomly with a mean (P) and standard deviation (SD) being specified:

TABLE 6. Fish submodel.

Component	Description	Units	Theory/assumptions	Source
Fish species	Lake trout (LT), brook trout (BT), lake whitefish (LW), ouananiche (LAS), artic char (AC), walleye (WA), Atlantic salmon (AS)		Only species of commercial or sport fishing value whose distribution is such that a substantial portion of their yield might be lost were considered. User specifies	
Fish assemblages	Lakes: BT, BT + LT, LT, LT + LW, LW, BT + LAS, LT + AC, BT + AC, BT + LAS + AC, AC; rivers: BT, AS + BT, AC, AC + LT, WA		Potential yields of some species vary according to the presence or absence of other species. A set of assemblages was assigned to represent the variation typical of Eastern Canada. User specifies	
Total potential yield	Total potential yield $YIELD = 1.4 \cdot (MEI)^{0.45}$	$kg \cdot ha^{-1}$	Yield is estimated for each lake using the morphoedaphic index	
MEI	Morphoedaphic index $MEI = TDS/\bar{z}$		MEI is an empirically derived formula that calculates potential fish yields as a function of a lake's total dissolved solids and mean depth. Is not suitable for rivers	Ryder et al. 1974
TDS	Total dissolved solids	$mg \cdot L^{-1}$	Allochthonous and autochthonous dissolved minerals within a lake. User specifies	
$\bar{z}$	Mean depth	m	User specifies	
Yield (species)	Allocation of total potential yield to each species within a lake's assemblage		Assemblage: proportion of total yield BT: 1.0, BT−LT: 3/0.7, LT: 1.0, LT−LW: 0.33/0.67, BT−LT−LW: 0.16/0.34/0.50, LW: 1.0, BT−LAS: 0.7/0.3, LT−AC: 0.2/0.8, BT−AC: 0.8/0.2, BT−LAS−AC: 0.4/0.5/0.1, AC: 1.0	Scientists with knowledge of specified assemblages best guesses
Minimum pH threshold	Minimum pH thresholds for recruitment failure when labile aluminum concentrations are zero		Humic system thresholds were used as a species' minimum threshold. A difference of 0.4 pH unit between humic and clear water system thresholds was assumed for species with unknown humic system thresholds. Species' thresholds: BT−4.5, LT−5.0, LW−4.0, LAS−4.7, AC−4.6, AS−4.7, WA−5.1. Chemistry submodel computes mean and spring pH	
e^a	Natural logarithm with exponent $a = 0.0015$ for all species			
Al_{free}	Labile aluminum concentrations		Chemistry submodel calculates labile Al	
Biomass	$B_{t+1} = (1 + p) \cdot S \cdot B_t - p \cdot S^2 \cdot B_{t-1} + w \cdot r$	$kg \cdot ha^{-1}$	A modification of Deriso's delay-difference population model. Keeps track of a pool of biomass which can increase in size due to growth and recruitment and decrease due to mortality	Deriso 1980
B_t	Biomass of stock in year t	$kg \cdot ha^{-1}$	Initial value calculated using estimated Y_t from MEI and h: Deriso parameter species specific BT(1.3), LT(1.01), LW(0.85), LAS(0.60), AC(0.92)	
p	Brody growth coefficient for weight	—		
S	Total annual survival	yr^{-1}	Deriso parameters species specific BT(0.28), LT(0.70), LW(0.60), LAS(0.4), AC(0.5)	
w	Weight at recruitment	kg	Deriso parameters are species specific. BT(0.22), LT(0.27), LW(0.50), LAS(0.09), AC(0.06)	

TABLE 6. (*Concluded*)

Component	Description	Units	Theory/assumptions	Source
r	Recruitment rate	Numbers	Initially calculated such that $B_t + L = B_t$ given other parameters. As lake chemistry changes affect recruitment and survival rates rather than yield directly, model allows user to explore the implications of impacts on these population processes	
Yield_{t+1}	Yield (in biomass) in year t $Y_{t+1} = h \cdot B_{t+1} = (1 + p) \cdot S \cdot Y_t - p \cdot S^2 \cdot Y_{t-1} + w \cdot r'$	$\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$		
h	Harvest rate		User specifies constant rate	
r'	Yield of new recruits in years $t + 1$ $r = r \cdot h = Y \times (1 - pS^2 - S - pS)/W$	Numbers	Estimated from the model using the constant yield predicted from the MEI equation	
$\text{pH}_{\text{threshold}}$	$\text{pH}_{\text{threshold}} = \text{minimum threshold} \cdot e^{a \cdot [\text{Al}_{\text{free}}]}$		Changes in pH and labile aluminum concentrations were assumed to only affect recruitment. Recruitment failure was expected to occur below specified pH thresholds	

TABLE 7. Scaling parameters required for the ELA region (watershed 5PD).

Lake area class (ha)		
1–10	10–100	100–1000
4652	20 769	31 600

	Distributions				
	Interval	Assumed value	Proportions		
A_W/A_0 ratio	0–5	2.5	0.14	0.47	0.80
	5–10	7.0	0.35	0.34	0.16
	>10	15.0	0.51	0.19	0.04
Mean depth (m)	0–5	2.0	0.83	0.69	0.48
	5–10	7.5	0.16	0.29	0.34
	>10	15.0	0.01	0.02	0.18
DOC ($\text{mg} \cdot \text{L}^{-1}$)	0–5	4.0	0.07	0.27	0.54
	5–10	8.0	0.56	0.67	0.43
	>10	13.0	0.37	0.06	0
TDS ($\text{mg} \cdot \text{L}^{-1}$)	0–35	20.0	0.36	0.5	0.44
	35–105	70.0	0.26	0.33	0.44
	>105	150.0	0.38	0.17	0.12

$$\text{Flushing rate} = \frac{P \cdot \text{WR} \cdot (A_W + A_0)}{\bar{z} \cdot A_0}.$$

Newbury and Beaty (1980) have shown that water renewal efficiency (WR) is satisfactory for describing the ratio of runoff to precipitation and that the proportion of lake area in the drainage is unimportant. This model is the same as the reduced HSM-H one.

This approach to hydrological budgeting for lakes has been widely used in eutrophication studies (Dillon and Rigler 1974). All lakes are treated as headwaters and the importance to acidification of the lags due to chains of lakes in drainage networks has not been considered.

TABLE 8. Parameters for the scaled model Muskoka–Haliburton scenario.

Precipitation ($\text{m} \cdot \text{yr}^{-1}$)	
Mean	0.99
SD	0.15
Outflow ratio	0.4
Rain pH	4.2
Initial alkalinities ($\mu\text{eq} \cdot \text{L}^{-1}$)	150
AAG ($\mu\text{eq} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$)	119
Area of lakes	
1 – 10 ha	13 387
10 – 100 ha	36 704
100 – i000 ha	47 798

Neither model is able to simulate the seasonal variation in runoff, although the ESSA model does use factors to describe the ratios of maximum monthly precipitation and runoff to annual precipitation and runoff, when trying to predict freshet pH/alkalinity depressions.

In both models, acid deposition is calculated using precipitation and annual mean precipitation pH. There is the suggestion that mean precipitation pH in Ontario may be lower in wet years (P. J. Dillon, OMNR, pers. comm.), supporting the idea of constancy in annual deposition. In models it would be better if deposition and precipitation were introduced separately.

Physico-Chemical Component

The main difference between the HSM-H and ESSA models lies in how the acid neutralizing capacity or alkalinity generation of the watershed is calculated. In the HSM-H model, it is based on assumptions about the soils in the watershed. In the

TABLE 9. Proportional distribution by lake types for brook trout assemblages. Assemblages assigned from analysis of Ontario Ministry of Natural Resources lake inventory data base and Minns (1981).

TDS ($mg \cdot L^{-1}$)	Mean depth (m)	Area (ha)	Lake type: Brook trout only	Lake type: Brook trout and lake trout	Lake type: Brook trout, lake trout, and lake whitefish
0–35	0–5	1–10	0.422	0.004	0
		10–100	0.254	0.015	0
		100–1000	0.058	0.013	0.013
	5–10	1–10	0.556	0.028	0
		10–100	0.259	0.120	0.011
		100–1000	0.051	0.055	0.037
	>10	1–10	1	0	0
		10–100	0.203	0.153	0.017
		100–1000	0.033	0.075	0.033
35–105	0–5	1–10	0.288	0	0
		10–100	0.112	0.003	0
		100–1000	0.025	0	0.004
	5–10	1–10	0.395	0	0
		10–100	0.175	0.023	0
		100–1000	0.013	0.019	0.013
	>10	1–10	0	0	0
		10–100	0.070	0.139	0
		100–1000	0	0.069	0.023
>105	0–5	1–10	0.246	0	0
		10–100	0.122	0	0
		100–1000	0.026	0	0
	5–10	1–10	0.514	0	0
		10–100	0.141	0.013	0
		100–1000	0.053	0.026	0
	>10	1–10	0.500	0	0
		10–100	0.167	0	0
		100–1000	0.176	0	0.118

ESSA model, it is based on the assumption that lake chemistry reflects watershed conditions and so back-calculations can be made. The HSM-H model assumes there are three sources of lake alkalinity: runoff, groundwater, and autochthonous (internal). In the ESSA model, runoff and groundwater sources are implicitly combined in the alkalinity generation (AAG), and internal sources, autochthonous or otherwise, are assumed to be zero.

In the HSM-H model, runoff alkalinity is determined by the availability of cation exchange sites, i.e. percent base saturation, which can be reduced by hydrogen ion loading. Analysis of the predictive equations reveals that decreases in base saturation are only important at high $[H^+]$ loading rates (Fig. 8). Renewal of the cation exchange capacity of the soils (CEC) by weathering was not included. There are suggestions that weathering increases with acid loading (Henriksen 1983). Therefore, while base saturation may be used to estimate runoff alkalinity, it is unlikely it need be treated as anything other than a fixed pool. Thus, the net result may not be any different from that of the ESSA model. If the CEC is depletable, renewal should be included or the model would exaggerate the worst case predictions.

The step from base saturation to alkalinity in the HSM-H model involves assuming a value (3.0) for the partial pressure of CO_2. There is considerable uncertainty about this choice (Thompson 1982) and resulting alkalinities are sensitive to that choice (Fig. 9).

TABLE 10. Group statistics for the ratios R_R/P_R and E_R/P_R.

Component	Group	No.	Mean ratio	SD
Runoff/precipitation R_R/P_R	1	13	0.39	0.05
	2	17	0.50	0.03
	Overall	30	0.45	0.02
Evaporation/precipitation E_R/P_R	1	16	0.62	0.02
	2	14	0.84	0.07
	Overall	30	0.72	0.12

The groundwater contribution to alkalinity (HSM-H model) is greatest in lakes with a small A_0 and a high A_W/A_0 ratio, with the magnitude being determined by the choice of hydraulic velocity, H_V (Fig. 10). However, a high A_W/A_0 brings a much higher runoff contribution and therefore the relative contribution from groundwater is minimized. On the Shield, groundwater is generally found at great depths. Geometric mean depths for three Shield regions, and three types (overburden, bedrock, and perched), range from 17.0 to 31.5 m (D. Beals, pers. comm.). Thus, it is unlikely that most Shield lakes, especially shallow ones, have any significant groundwater input. Some authors (Eilers et al. 1983; Bottomley et al. 1984) have argued that groundwater is important even in small lakes. The matter is not resolved.

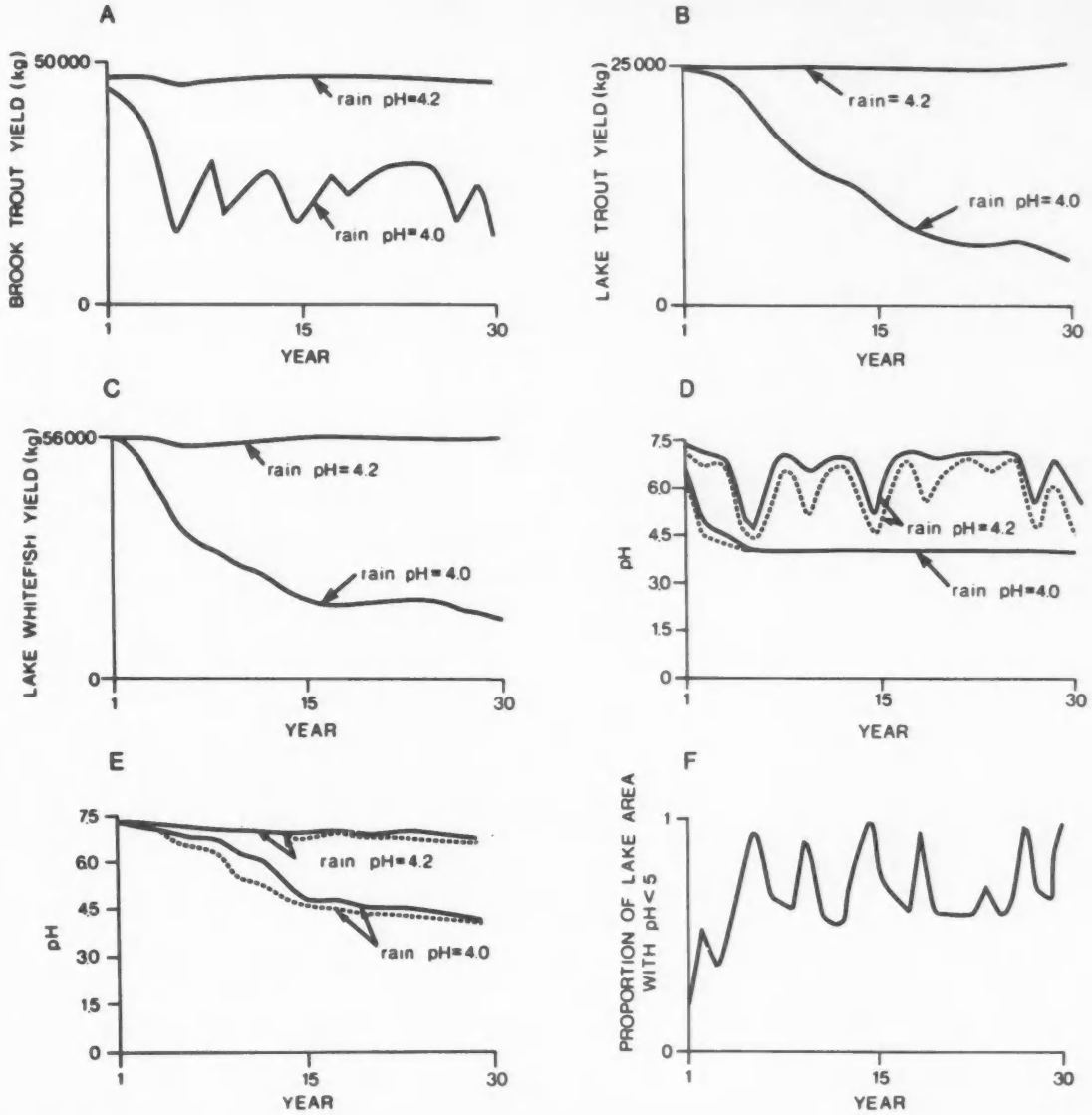

FIG. 7. Scaled model for the Muskoka–Haliburton region. (A) Brook trout yield; (B) lake trout yield; (C) lake whitefish yield; (D) pH in a small, shallow, small watershed lake (—, mean pH; ---, maximum pH); (E) pH in a large, deep, small watershed lake; (F) proportion of lake area with pH < 5.0.

Internal autochthonous alkalinity (from Table 1) could account for the entire lake's alkalinity, seemingly an unlikely situation; calculation of this component using primary production would reduce the estimates. Net primary production is normally only a small proportion of gross primary production. Flushing rate also has an influence on the contribution of autochthonous production in the HSM-H model. In the lakes with only lake trout, with annual flushing, the contribution is 17 $eq \cdot L^{-1} \cdot yr^{-1}$. If the flushing rate is 0.1 $\cdot yr^{-1}$, the contribution is 170 $eq \cdot L^{-1}$. One might expect a slowly flushing lake to have lower primary productivity, reflecting lower nutrient inputs and perhaps a more complete reuse of organic carbon, thereby minimizing the net alkalinity contribution. However, higher flushing rates may dilute standing stocks and reduce productivity. The importance of this component has not yet been properly evaluated. The same is true for other internal H^+ consumers such as sulphur bacteria. In the ESSA model, internal autochthonous alkalinity was not included because it was considered small.

In the ESSA model, several alternate ways of estimating the actual alkalinity generation, AAG or ANC (see Table 5), of the watershed were used. In the first formula:

$$AAG = RAG \cdot (1 + (C - 1) \cdot 10^{3.5pH})$$

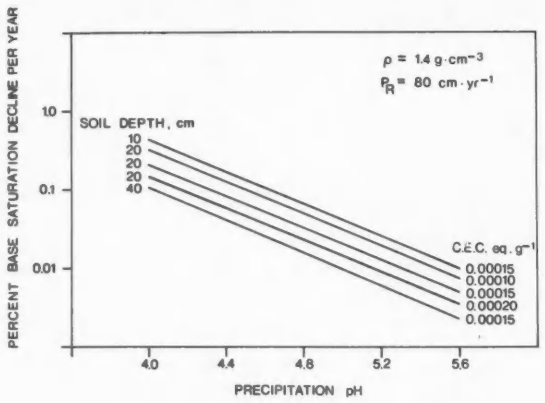

FIG. 8. Percent change in base saturation relative to precipitation pH given various assumptions concerning soil depth or cation exchange capacity (CEC).

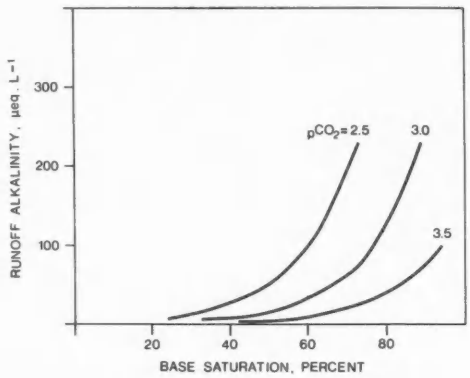

FIG. 9. Relationship between base saturation and alkalinity at three levels of pCO_2.

with C being the ratio of expected AAG with rain of pH 3.5 and RAG. This was an empirical way of allowing AAG to increase with increasing deposition pH. In a second formula:

$$\text{AAG} = \text{NAG} + D + m\,(D_t - D), \text{ if } D_t > D$$

where NAG = natural alkalinity generation, D = mean deposition meq·m^{-2}·yr^{-1} (milliequivalents per square metre per year), D_t = current deposition (milliequivalents per square metre per year), and m = proportion of excess deposition resulting in AAG. In this case, AAG is a function of D. A value of m less than 1 indirectly represents two processes: (1) increased deposition is not entirely compensated for by increased cation exchange and (2) reduced runoff pH will shift carbonate equilibrium away from natural alkalinity generation. Neither of these formulae is considered a reasonable representation. It may be unrealistic to assume that while AAG increases in periods of high deposition, it does not decline when lower than average D occurs. Another approach would have:

$$\text{AAG} = \text{NAG} + mD$$

such that m is less than 1. This would imply that there is always a portion of deposition on the watershed which is neutralized by cation exchange. Another possible weakness of this whole

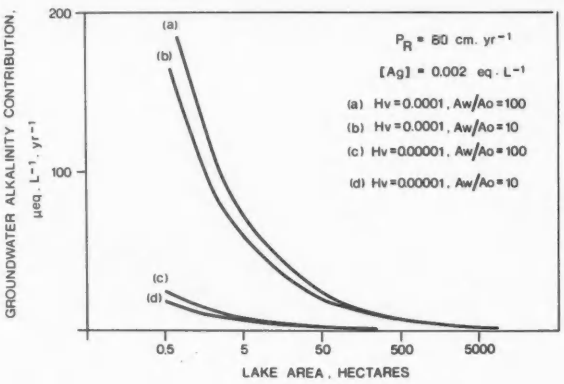

FIG. 10. Alkalinity contribution of groundwater in relation to lake area at a set of assumed values for H_V, (hydraulic velocity), and A_W/A_0 (drainage to lake area ratio).

approach is that AAG is considered to be independent of cumulative acid deposition. If the CEC pool is depletable (assumed in the HSM-H model), the ESSA model would underestimate the ultimate effects of acid deposition. This is an important difference between the two models, but may be extremely difficult to resolve from research programs.

One consequence of the formulation of the ESSA model is a prediction that lake alkalinity, at steady state, increases asymptotically with the watershed to lake area ratio. Comparison of observed and predicted alkalinities for the data set from the ELA and Muskoka–Haliburton areas did not support this contention. However, the absence of a good correlation may be partially due to a limited range of values for watershed to lake area ratios. The heterogeneous distribution of calcareous surficial materials between watersheds may overwhelm the effect of the A_W/A_0 ratio. A high A_W/A_0 ratio would yield more ANC on an annual basis and so produce a greater lake alkalinity. But, at the spring freshet, with runoff over frozen ground, high A_W/A_0 may be effective in reducing lake alkalinity. So, with the A_W/A_0 being a determinant of flushing, seasonal variation in the input–output of alkalinity may be very different from the average outcome. Conversely, a lake with a low A_W/A_0 ratio could have a lower input of ANC on average, and would be less affected by the spring freshet.

The ESSA model, predicated on an episode being a spring snowmelt, includes episodic alkalinity declines calculated as a function of mixing depth and the fractions of annual outflow, alkalinity generation, and deposition occurring in the month of minimum mean alkalinity. Episodic rain events would have to be modelled in a different manner, allowing for greater interaction between water and soil. The coincidence of these events with exposure of biota was not considered in detail.

In both models, lake pH values are predicted from alkalinity levels. With the ESSA model, DOC is a cofactor in the calculation. In the HSM-H model, the river pH – alkalinity equation was used to back-calculate lake pH. This has already been shown to be very sensitive to the assumption about pCO_2. In the ESSA model, an alkalinity–DOC equation was used as an approximation, even though it was known that aluminum hydroxides affect alkalinity, and other forms of aluminum effect electroneutrality causing titration curves to underestimate pH (Andrews et al. 1980; Driscoll and Bisogni 1984). Since pH is so often an important determinant of biological

effects in acidification models, every effort should be made to ensure a minimal error in using other data (e.g. alkalinity, DOC, $[A_L]$), to predict pH.

Although the models are built from quite different foundations (HSM-H the watershed, ESSA the lake), they have much in common. Both consider the effects of cation exchange on the ANC output of the watershed, although the HSM-H model assumes that the cation exchange will diminish with time. Both models centre on a balancing of the lake alkalinity budget with lake pH being predicted via equations from alkalinity. The HSM-H model includes terms for groundwater and internal alkalinity sources, but there is no clear evidence that they contribute significantly in nature. The ESSA model implicitly includes groundwater in its AAG term.

Fisheries Component

Both models dealt with several fish assemblages, used the MEI to predict yield, and used allocation/reallocation tables to distribute yield among species. The HSM-H model used pH as the only species extinction threshold, while the ESSA model used a combination of pH and aluminum to predict recruitment success. In practice, only annual mean values were used, although the ESSA model could use spring values.

The game fish assemblages used were different between the two models, reflecting zoogeographic differences between Ontario and the rest of eastern Canada. The frequency of occurrence of various assemblages were much less well known outside Ontario. For both models, the allocation of estimated yield between game species and others by assemblage was based on consensus among a small group of experts. Reallocation of yield from species made extinct by surpassing thresholds was also decided by consensus. There were little or no data from which allocations or reallocations could be estimated or confirmed.

In the HSM-H model, it was assumed that for the MEI, TDS could be replaced by alkalinity, after appropriate scaling. Therefore, when alkalinity in a lake declined because of acidification, potential fish yield declined as per a MEI-type function. Threshold pHs specified the extinction points for each game species. In the ESSA model, original TDS, assumed to be unaffected by acidification, was used to predict a lake's potential yield. TDS may in fact decrease with added acid inputs. Then, in each assemblage, the allocation tables were used to calculate original potential yield for each game species. The literature estimates of Walford growth parameters and survival for each species were used to parameterize a Deriso-type yield model (Deriso 1980) where recruitment was the only unknown. Recruitment success was then linked to mean annual pH and aluminum levels. So, in the ESSA model, yield was not assumed to decline along with alkalinity. Instead, once recruitment failed, yield declined gradually to zero with a rate determined by the growth and survival parameters.

It is important to note that MEI predictions are not very accurate, especially at the low alkalinity end (i.e. softwaters), being based on a relationship derived from a very wide range of TDS values. The MEI does not indicate maximum sustainable yield and, often, long-term average yields result from variable effort. In Ryder's original work, yield and alkalinity were strongly related over a wide range of alkalinity. However, there are no data available yet showing matched changes in yield and alkalinity. Of course, there are acid lakes with little or no fish yield.

The population approach, i.e. the Deriso-type model used by ESSA, serves to highlight the weakness of an approach based solely on MEI and allocation/reallocation tables. In the models used, the pH and/or aluminum thresholds were not clearly linked to the life history phases when effects occur. A better approach would rely on population models where links with acidification can be explicitly defined, e.g. through recruitment changes influenced by spring pH and aluminum levels. Species interaction could also be considered, e.g. through density-dependent functions, and an operationally defined maximum sustainable yield calculated. The step from laboratory-based toxicity thresholds to field predictions can, however, be difficult, as fish may avoid toxic conditions.

Neither of these models dealt with contaminant burdens whether as an auxiliary factor in population declines or as a factor limiting exploitation. Again, a population-based approach with size and age criteria would be better able to deal with uptake and accumulation.

Scaling

Large-scale risk assessment cannot be undertaken unless estimates of the total size of the resource and adequate characterization of lake size and watershed features are available. Since the two modelling exercises took place, watershed data in the rest of eastern Canada (a large lake inventory data base existed in Ontario) have been prepared by the Department of Fisheries and Oceans, and localized inventories of fish assemblages and lake chemistry and morphometry have been identified.

As regards the actual scaling process in model simulations, the use of variable classes which are unrealistically wide introduces errors. In the HSM-H model, lake and watershed areas were in class values spaced by orders of magnitude (from Cox 1978). Subsequent analysis (Minns 1984) showed that these class values poorly represented the lake population structure. The ESSA model took a similar approach to that of the HSM-H model. Scaling categories should be set up to ensure that the most sensitive ranges of key parameters are well represented. Also, only limited consideration was given to possible correlations among variables, such as AAG, TDS, DOC, lake area, mean depth, watershed area, and perhaps the distribution of certain fish species, e.g. lake trout do not occur in shallow lakes. A number of weak correlations, if ignored, can result in highly erroneous predictions.

General Discussion

When assessing the performance of any model, there are a number of questions that have to be addressed. The nature of those questions will depend on whether the model was constructed to make predictions or to test our understanding of the system (perhaps, in order to identify data gaps and research priorities). Obviously, a major objective is to predict impacts of acidic precipitation on the fishery resources in sensitive regions. In the mean time, our objective was to develop a sound methodology which could improve iteratively as new data and new concepts are put forward. In the case of the two models assessed here, it may be appropriate to ask both sorts of questions, given that there are no antecedents for this class of model.

If we are challenging the predictions of such a model, i.e. a regional impact assessment, the questions posed might take the following form.

(i) Are the predictions of the chemical model consistent with

observations of the response of lake and stream chemistry to anthropogenic acidic loading?

(ii) Does the fisheries model accurately predict changes in fish assemblage productivity and species composition, observed in lakes undergoing acidification?

(iii) Does the scaling model accurately reflect the observed intraregional heterogeneity with respect to lake or stream chemistry and fish assemblages?

The quick answer to all three questions for both models is *NO*. The reason for such an answer exists more from the observational data available to us than in the structure and equations of the models. We have hardly any data series where the lake chemistry and fisheries changes have been well documented during the course of acidification (exceptions being Mills (1984) and Schindler et al. (1985)). The challenge for models like these is to predict the response to a marked change in the input conditions accurately. At ELA in northwest Ontario (Schindler et al. 1980; Mills 1984; Schindler et al. 1985), a whole lake was *experimentally* acidified over a number of years and the biological response assessed. Such an experiment provides some insight into the accuracy of the fishery models, but yields limited insight into the chemical model and very little insight to the scaling models. In Norway, a limited number of small watersheds are being exposed to either increased or decreased sulphate loading to assess the response of stream chemistry to *changing* loads. Again, this only challenges the chemical models. In Ontario, a limited number of watersheds, each containing a few hundred lakes, are being surveyed intensively to obtain more detailed knowledge of intraregional variability. This is a challenge for the scaling model. However, at the time of these two modelling exercises, *none* of the results of the above studies was available! Certainly, nowhere are all three submodels being challenged simultaneously, except perhaps in the vicinity of Sudbury, where taller smokestacks and reduced levels of smelting have altered emissions. The available historical data, changing conditions, and limited area of effect would provide an excellent test of model performance.

If we are looking for data gaps and research priorities, the questions take another form.

(i) Which functional links or parameter values are least well known and yet critical to the predictions?

(ii) Which extensive data needs are poorly dealt with in existing data bases?

(iii) What are the relative precisions required for various parameters given their interlinkage?

(iv) Are there components of the models which are not contributing to the extensive prediction of impacts?

(v) Are there components which are not present in the models, but should be, as they will contribute significantly?

(vi) Does the model predict the things we want to predict?

To these questions, the answer is qualified, *but positive*. We do not know if there is erosion of fisheries productivity, as alkalinity declines before the more obvious symptoms of missing year-classes and species extinctions occur. We are not sure if the laboratory-derived pH and aluminum thresholds for fish mortality can be applied to natural systems. We do not know if the target fish species are exposed to threshold or worse conditions. In the HSM-H model, cation exchange capacity is assumed to decline with no provision for replenishment via weathering. In the ESSA model, we do not know the source of the generated alkalinity or how acid loading may affect its generation. The scaling data did not exist for large areas of eastern Canada. The class sizes and selection of key variables could introduce bias and errors to predictions. The models will predict how many lakes become acid, and in one case (brook trout), predicted the decline in fishery productivity (as it was expected to occur).

The modelling exercises did influence research and data-gathering priorities. More effort has been directed to characterizing intraregional lake variability, field tests of the toxicity of lake conditions to fish, and the assembly of adequate watershed data on lakes in different regions of eastern Canada.

Chemical Models

Taken together there are a number of areas where neither model was satisfactory. First, there is the question of whether cation exchange capacity in the watershed significantly alters the acidification process. Arp (1983) presented an approach similar to that of the HSM-H model, but included weathering which could be a significant source. In the empirical models such as ESSA's, the so called "*F*" factor of Henriksen (1982) represents the cation exchange process whereby a proportion of the incoming acid is neutralized by cation exchanges, although the capacity is assumed to remain constant. Oliver and Kelso (1983) have shown that a sort of cation exchange takes place between the water column and the sediments in the lakes and could be important for, particularly, poorly buffered systems. A second factor, sulphate retention in the watershed, was not considered in either model, although related to the cation exchange question. Christopherson et al. (1984) showed that some watersheds will accumulate sulphate over time, ultimately coming into steady state of input versus output. This implies a delayed acidification response in lakes, although the final result may be the same, especially if the sulphate accumulation capacity is limited as might be expected in Shield areas.

The role of natural acidity, i.e. due to humic acids, was not adequately addressed, although in the ESSA model consideration of labile aluminum did incorporate the impact of dissolved organic matter, which mitigates toxic effects of aluminum.

There is no clear evidence on the role of biotic contributions to the lake alkalinity budget. While it is true that photosynthesis results in the production of alkalinity, the reverse process, usually aerobic respiration, consumes alkalinity. It is generally considered that net primary production is only a small proportion of gross. Under anaerobic conditions, reduction of ions (SO_4, NO_3, Mn, Fe) will produce alkalinity (U.S. EPA 1984).

At the time the models were developed, there was very little evidence regarding the role of groundwater on the shield. Newer evidence is equivocal, although it appears it would be rash to dismiss groundwater involvement. Perhaps in the short term, most attention should be devoted to headwater Shield lakes with minimal groundwater influence.

Current research programs in Canada, particularly in the so-called "calibrated watersheds" at ELA (northwest Ontario), Turkey Lakes (north central Ontario), Dorset (southern Ontario), Lac Laflamme (Quebec), Kejimkujik (Nova Scotia), and in the United States and Europe, are addressing many of these questions. In the short term, we will have to continue to rely on empirical models for guidance. The ESSA model is based directly on the approaches of Henriksen (1979 and 1980), Almer et al. (1978), and Kramer and Tessier (1982). The HSM-H model has features in common with the models of Booty and Kramer (1984) and Arp (1983).

The models of Henriksen (1979, 1980), Almer et al. (1978), and Kramer and Tessier (1982) are all based on statements of ionic balance (Lung 1984) and assume steady-state conditions

in completely mixed water bodies. They are descriptive models rather than functional models which predict the chemical behaviour over time. Henriksen (1982) modified his model to account for probable changes in base cations resulting from acidification. Thompson (1982) introduced a time element into the model by calculating ionic balance budgets for rivers. This model assumes that the "cation denudation rate" (CDR) is equal to the sum of excess sulphate output and bicarbonate output. Of course, we do not know what the CDR would be in the absence of excess sulphate loading.

More recently, a number of more intricate models have been proposed, e.g. U.S. FWS (1982), Arp (1983), Christopherson et al. (1984), Booty and Kramer (1984). These models go into much greater detail in their hydrological description of watersheds, their description of soil chemistry, and chemical transformations. They try to predict chemical dynamics over time in streams and lakes. However, until such models, simple or intricate, are calibrated with good time-series data, and/or causal mechanisms are unravelled, the rate of acidification will remain the major unknown.

Fisheries Models

In the introduction we identified five areas of concern regarding the effects of acidification on fisheries. Three (ii, iii, and v) are considered in the HSM-H model, while only two (iii and v) are in the ESSA model. All five impacts can cause loss of recreational and economic benefits. However, it may be that (i) to (iii) can occur in a much larger portion of the total resource and consequently add up to a far greater overall impact. There is limited evidence that contamination is enhanced by acidification (Suns et al. 1980; Kelso et al. 1982), but there is little evidence that erosion of productivity is occurring.

The extinction of species assemblages is irreversible, as unique gene pools are lost. This and the incidence and result of episodic mortalities must remain one of the priorities for prediction. The extent of production loss above acute mortality losses is largely unknown. A decline in production from year-class losses might be predicted more accurately in small rather than large lakes, as large lakes are more likely to have "chemical" refuges, more subpopulations which could compensate for varying success, and greater diversity among spawning areas. Since lake morphometric variables are continuous through several orders of magnitude, the subsequent extent of impact could vary from minor loss of recruitment through partial loss of eggs, larvae, or fry, to loss of an entire year-class. Compensatory changes in growth and survival could ameliorate the effect on yield. Similarly, other fish species may increase their contribution to yield. Qualitative changes in fish assemblages probably reduce fishing opportunities and yields. Current research efforts are largely focussed on identifying toxicity thresholds. As a consequence, modelling efforts are relying on prediction of episodic mortalities and extinction of selected fish species. Some research on the question of declining fish production and acidification is underway (GLFRB, OMNR). The fisheries models can incorporate the results as they appear.

The use of a modified MEI (with alkalinity rather than total dissolved solids) in the HSM-H model incorporated the following assumptions: (i) that MEI is a good predictor of yields for Shield lakes and (ii) that a decline in productivity follows a loss of alkalinity. Most fisheries scientists have some confidence in MEI as a predictor of fish yield in unpolluted lakes, although they appreciate the crudeness of estimates especially at low MEI levels. However, scientists show little empathy with the hypothesis that a modified MEI reduced by acidification leads to reduction in fish yield. Better resolution can only come from studies designed to measure the factors that predict yield, production, or biomass of fish assemblages in lakes at various stages of acidification. The evidence thus far suggests that MEI is not a useful predictor in shield lakes (Hanson and Leggett 1982; Prepas 1983; Kelso 1985). It may be that a simple morphometric parameter such as mean depth will suffice, perhaps modified by pH (with or without aluminum), as has been found for lake trout lakes in Ontario (G. Beggs, OMNR, Queens Park, Toronto, Ont., pers. comm.).

Another component that is poorly known, especially outside Ontario, is the distribution and frequency of occurrence for fish species of concern. Although it may be possible to estimate the sizes of lakes in a region, and to ascribe likely chemical conditions based on extensive surveys, it is only possible to know the occurrence of fish species in very few lakes. Further, there are as yet very few models that can use simple lake attributes to predict the likelihood of presence or absence of particular fish species.

Predictions of LRTAP Impacts

Through the iterative process of model building and assessment, objectives for assessing and predicting the large-scale impact of acidic deposition can be refined and our research priorities clarified. The two models described here were developed to improve methodology. We retain the aim of being able to make accurate predictions of future impacts of acidic precipitation on the freshwater fishery resource in eastern Canada.

Models draw together the best of our theories and experimental and survey data. Our ability to calibrate models is constrained at present because of a shortage of time-series data with both limnological and biological observations. Synoptic lake survey data are available from several sources although important parameters are often omitted. Many agencies are now working toward a better balance of synoptic and time-series data gathering. Case histories for lakes and rivers give expression to the complex interactions which are only hinted at in simulation models. As the field evidence becomes stronger, so the model predictions of extensive impacts will improve. As the predictions improve, so they will come to influence public policy. The decision-making process must be dependent on the unanimous acceptance of the assessments and not on the emotions of people or the tides of politics.

We know that acidic precipitation is a problem. The uncertainties lie in such questions as: "How extensive will the impact be?" and "How long do we have before action will be too late?" The building of models such as these can address the broader issues, and speed the process of reducing uncertainty. The iterative process must continue until the problem is resolved. Already we are in a third iteration.

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BOOK REVIEWS / COMPTES RENDUS

Rare, Endangered and Extinct Fishes in Canada. *Don E. McAllister, Brad J. Parker, and Paul M. McKee. Syllogeus 54. National Museum of Natural Sciences, Ottawa, Ont. 1985. 192 p., 60 figs. including 36 distribution maps. No charge. ISSN 0704-576X.*

It might be said that a concept falls into the category of general knowledge when it is alluded to in a weekly newsmagazine. In an article entitled "Canadians as endangered species," Amiel (1985) spoke of "environmentalists going into apoplexy over the possible extinction of the snail darter or whooping crane...." If rare and endangered Canadian fishes are general knowledge, it is largely the result of the work of the authors of the publication reviewed here. Their work on this topic began in 1970 (McAllister 1970), and included an early and major report on 13 fishes in southern Ontario (Parker and McKee 1980), the area concerned in regard to the largest number of rare and endangered species. In 1982 (McKee and Parker 1982), they published a report for four cyprinids and a fundulid. In 1984, Parker and McKee wrote four of 10 status reports which were published in a special section of an issue of the Canadian Field-Naturalist (Vol. 89, No. 1).

This publication is basically a discussion of 37 Canadian forms including species, subspecies, and forms as yet unnamed (two whitefishes, one sucker, and one stickleback). Only two of the species are marine fishes (*Sardinops sagax caerulea* and *Allolumpenus hypochromis*), and they are classified only as rare, suggesting at present that the marine environment is safer, or that we know less about the status of marine species.

The authors' rationale for the publication is "a wish to bring some facts to the public's attention, while there is yet some chance of remedial action." It was their hope that the text would be "easy to read for the public and sufficiently authoratative for the scientist." For those readers not bombarded by all the other reports, I believe they have achieved their aim in this summary publication.

More information is provided than the reader might infer from the title alone. The species accounts are organized under the headings Canadian status, status elsewhere, taxonomic status, distinguishing features, habitat, biology, protective measures taken, and recommendations. One of the strengths of this publication is the number, and the highly specific nature, of the detailed recommendations made for remedial measures. These range in various species from stopping industrial damage to environments, to determining impact of bait dealers, to need for taxonomic or biological studies. Another strength is the inclusion of status elsewhere. That helps the reader interpret status assigned by various levels of political organizations. In this way, the reader better understands the status assigned to Canadian populations which are usually at the northern extreme of the total distribution of the species.

Although not indicated in the title, the biology sections are very broad in scope, and for some species include even growth tables and values for various environmental factors.

The general introduction is historical, starts with prehistorical inhabitants, and includes such themes as man's general impact on the freshwater environment, acid precipitation and its effects on fishes, and lumbering. It ends with recommendations covering topics such as legislation, green buffer strips, wetlands and channelization, toxic spills, and forestry practises. The weak base in law and low level of financial backing of the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) is contrasted with that of the U.S. Endangered Species Act 1973.

The authors state that the publication is in less than perfect or complete form, thereby ending any need to point out small problems in a review.

The text ends with a list of 20 species for which the authors suggest that assignment of status might be likely in the near future. Some of these suggestions exhibit the problem of assignment of status in the face of inadequate knowledge of limited and local distribution. The grass pickerel, *Esox americanus vermiculatus*, is listed, with the apparent justification of the confirmation of its existence in one upper Niagara River tributary. That subspecies is very abundant in many tributaries to that river and in several other isolated situations tributary to Lake Erie, Lake Ontario, and the St. Lawrence River.

Most species are illustrated with large detailed line drawings. The quality is variable. For some it is very high, and for others not so high (e.g. the spotted sucker has no "spots"). It is probably only personal preference, but I am bothered by series of portraits in which sturgeons and small cyprinids are all illustrated full width of the page. The large size of the smaller fishes makes obvious certain missing details that would not be apparent, or needed, otherwise.

The need for concern, and for status, is usually based on restricted distribution. More detailed distribution maps may have been more appropriate, but the half-page Canada-wide map for each species provides a general idea of the location of the form.

Nomenclature becomes confusing in the variety of these extant endangered fish reports. Salish sucker of this publication was listed not long ago as Campbell sucker. While I am aware that we must protect rare things quickly, I am, however, wary of assigning an official status to an unnamed form which, with more opportunity for study, could turn out not to be distinct from an existing species. I was also disappointed by the continuance here of the unilateral change in the common name of the Atlantic whitefish (to Acadian whitefish), in conflict with that originally applied and that given in other standards such as the names list (Robins et al. 1980) and the atlas (Lee et al. 1980). In fact, readers of these lists and status reports are often left wondering about the lack of agreement. Several species that were on previous lists are included in this publication only in the general introduction. Some of these variances result from changed status, and others from individual judgment by various authors. Local, unnamed forms (e.g. Opeongo whitefish) are included in this publication (as rare, threatened, or endangered), but the unique Lake Ontario population of Atlantic salmon, *Salmo salar*, is not included among the extinct forms. By using the words "Canadian fishes" in the title, this pub-

lication avoids one serious terminological problem which has occurred when smaller jurisdictions prepare lists of local endangered "species." Local lists should be referring to endangered local populations of the various species, since the species might occur elsewhere in vast numbers.

In the special section on rare and endangered fishes of the issue of Canadian Field-Naturalist mentioned earlier, Cook and Muir (1984) reviewed the history of this concern in Canada, and Campbell (1984) reviewed deliberations on Canadian fishes and COSEWIC. The many forms in which information on rare and endangered fishes is appearing are highly duplicative, derived from the same limited literature, uneven, and often confusing. It is especially confusing to those of us asked to read status reports prepared by COSEWIC for Canada, and those on the same species prepared by the International Union for Conservation of Nature and Natural Resources (IUCN). The two organizations use different terms for levels of status. These differing evaluations result in a Canadian fish being designated rare by COSEWIC, but endangered by IUCN. Campbell (1984) listed 50 Canadian species that were under various levels of consideration. In contrast, Ono et al. (1983), indicated only six fishes for Canada. McAllister and co-authors give the status of *Coregonus nigripinnis* as extirpated except in Lake Nipigon, but the COSEWIC status "extirpated" is defined by COSEWIC as "any indigenous species of fauna or flora no longer existing in the wild *in Canada* but existing elsewhere."

There is obvious need for more standardization and more international coordination in the various considerations of status for endangered plants and animals. In any regard, it is very useful for a wide range of readers to have this summary available in one publication. It does, however, carry a responsibility to keep the information up to date.

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E. J. CROSSMAN

Department of Ichthyology and Herpetology
Royal Ontario Museum
100 Queen's Park
Toronto, Ont. M5S 2C6

(R637)

BOOKS RECEIVED/LIVRES REÇUS

El Niño North: Niño effects in the Eastern Subarctic Pacific Ocean. *Warren S. Wooster and David L. Fluharty (editors). Washington Sea Grant, Seattle, WA. 1985. 312 p. Paperback only, $10.00 (U.S.). ISBN 0-934539-01-4.* This book brings together papers presented at the Pacific Marine Environmental Laboratory, Seattle, in September 1984 on Niño effects along the west coast of North America, with particular attention being given to the region extending from northern California to the Gulf of Alaska. In 12 contributions, changes in the physical environment, both atmospheric and oceanic, are described. Another 12 papers consider the biological response to these changes, with topics ranging from plankton, shellfish, and seabirds through larval and adult fishes, including the consequences for management of salmon fisheries. A selected bibliography is also included. [R707]

Trout farming handbook. 4th ed. *Stephen Drummon Sedgwick. Fishing New Books Ltd., Farnham, Surrey, England. 1985. 160 p. £10.00. ISBN 0-85238-135-2.* This edition was written to bring the principles of trout culture up to date. The original book was revised throughout and additional chapters added. Included are descriptions of techniques, methods to avoid pollution, and advice on cost effective planning. [R708]

Freshwater ecosystems: modelling and simulation. *M. Straskraba and A. Gnauck. Developments in environmental modelling, 8. Elsevier Science Publishers, Amsterdam. 1985. 300 p. $77.75 (U.S.) ISBN 0-444-99567-6. Available from Elsevier Science Publishers Co. Inc., New York, NY.* The authors introduce new holistic, particularly cybernetic, concepts in ecosystem theory and modelling of freshwater ecosystems which cover methods, subsystem models, applications, and theoretical developments. Part I begins with a brief introduction to the principles of systems theory and their applications to ecosystems, and provides a summary of various methods of systems analysis. In Part II, emphasis is laid on the pelagic processes in standing water, characterized by relatively uninvolved structures from which models can be readily developed. Part III describes applications of the technique of modelling to solutions of theoretical and practical problems, with different modelling methods and objectives being used in the various chapters. These descriptions provide a good account of the variety of possible approaches and applications. More recent developments in the methods and theory of ecosystem modelling are covered in Part IV which also includes a discussion of future trends. [R709]

A hatchery manual for the common, Chinese and Indian major carps. *V. G. Jhingran and R. S. V. Pullin. ICLARM Studies and Reviews II. Asian Development Bank and International Center for Living Aquatic Resources Management, Manila, Philippines. 1985. 191 p. $10.00 (U.S.) (airmail). ISBN 971-1022-17-6.* This manual provides practical guidance to carp hatchery workers and background information on carp biology and culture. Information sources include the author's personal experiences and knowledge, published literature, and secondary sources. [R710]

Atlantic fishing licence directory/Annuaire des permis de péche de l'Atlantique. *Canadian Special Publication of Fisheries and Aquatic Sciences 79. 1986. 931 p. $24.95 (Canada), $29.95 (Other countries). ISBN 0-660-53032-3, ISSN 0706-6481.* A listing of Atlantic coast fishermen (full-time or part-time) and fishing vessels that participated in the domestic commercial fishery on the Atlantic in 1984 and the limited entry fisheries. [R711]

The Atlantic salmon in the history of North America. *R. W. Dunfield. Canadian Special Publication of Fisheries and Aquatic Sciences 80. 1986. 181 p. $11.95 (Canada), $14.35 (Other countries). ISBN 0-660-11923-4, ISSN 0706-6481.* The Atlantic salmon was a principal food source for the Amerindian cultures which shared its range. It became increasingly important in the life of developing colonies but now has a declining presence. This history also documents instances of overexploitation and careless destruction of stocks and their environment. [R712]

Transactions of the 1984 Canadian Sport Fisheries Conference: Canada's Sport Fisheries — getting ready for the 1990's. *A. L. W. Tuomi (editor). Canadian Special Publication of Fisheries and Aquatic Sciences 82. 1986. 338 p. $15.00 (Canada), $18.00 (Other countries). ISBN 0-660-53109-7, ISSN 0706-6481.* The proceedings of a conference seeking consensus by the major sectors of the industry on overall goals and programs for Canada's sport fisheries. [R713]

Analysis of test and flight data from the Fluorescence Line Imager. *Gary A. Borstad, H. R. Edel, J. F. R. Gower, and Allan B. Hollinger. Canadian Special Publication of Fisheries and Aquatic Sciences 83. 1986. 38 p. $6.00 (Canada), $7.20 (Other countries). ISBN 0-660-11960-9, ISSN 0706-6481.* The report describes the planning and analysis of test and flight data from the Department of Fisheries and Oceans' Fluorescence Line Imager, a programmable imaging spectrometer designed for high sensitivity and high spectral resolution. [R714]

Guide to the freshwater aquatic microdrile oligochaetes of North America. *R. O. Brinkhurst. Canadian Special Publication of Fisheries and Aquatic Sciences 84. 1986. 259 p. $14.95 (Canada), $17.95 (Other countries). ISBN 0-660-11924-2, ISSN 0706-6481.* Five families containing some 150 species are reviewed. Keys and brief descriptions together with illustrations are provided for all species known from Alaska and Canada to the southern border of the United States. The evolution and classification of the Oligochaeta are reviewed. [R715]

ANNOUNCEMENTS/AVIS

Wildlife Toxicology Fund

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(1) Effets des produits chimiques utilisés en agriculture ou en sylviculture sur la faune
(2) Effets des polluants industriels toxiques sur la faune
(3) Évaluation du succès des mesures adoptées pour atténuer les effets mentionnés en 1 et 2
(4) Mise au point et mise en oeuvre de techniques qui utilisent des espèces fauniques comme indicateurs de la présence de produits chimiques toxiques dans l'environnement
(5) Détermination des processus environnementaux par lesquels les substances toxiques peuvent agir sur la faune

Le fonds pour la toxicologie faunique est un programme coopératif qui assume jusqu'à la moitié du coût des projets de recherche approuvés, à condition que l'on puisse trouver auprès d'autres sources des fonds équivalents. Pour de plus amples informations, veuillez communiquer avec le Secrétaire, Fonds pour la toxicologie faunique, a/s Fonds mondial pour la nature Canada, Suite 201, 60 St-Clair Avenue est, Toronto (Ont.) M4T 1N5. Téléphone : (416) 923-8173.

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